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STUDIES IN ARTOCARPUS AND ALLIED GENERA, III. A REVISION OF ARTOCARPUS SUBGENUS ARTOCARPUS

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Artocarpus J. R. & G. Forster, Char. Gen. 101. *t. 51, 51a.* 1776, nomen conservandum; Linn. f. Suppl. Pl. 61, 411. 1781; Lamarck, Encycl. Méth. 3: 207. 1789; Willd. Sp. Pl. ed. 4. 4: 188. 1805; Persoon, Syn. Pl. 2: 531. 1807; Blume, Bijdr. 479. 1825; Roxb. Fl. Ind. 3: 521. 1832; Blanco, Fl. Filip. 666. 1837, "*Arctocarpus*"; Trécul, Ann. Sci. Nat. Bot. III. 8: 109. 1847; Miq. Fl. Ind. Bat. 1(2): 284. 1859, Suppl. 417. 1861, Ann. Mus. Lugd.-Bat. 3: 211. 1867; King in Hook. f. Fl. Brit. Ind. 5: 539. 1888; King, Ann. Bot. Gard. Calcutta 2: 1. 1889; Becc. For. Borneo, 625. 1902; Renner, Bot. Jahrb. 39: 363. 1907; Elmer, Leafl. Philip. Bot. 2: 609. 1909; Gagnep. Bull. Soc. Bot. Fr. 73: 86. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 731. 1928; Corner, Wayside Trees of Malaya, 649. 1940; Jarrett, Jour. Arnold Arb. 40: 8, 11. *fig. 1, f–k, fig. 3, d–f.* 1959. TYPE SPECIES: *Artocarpus communis* J. R. & G. Forster.

Saccus or *Soccus* Rumph. Herb. Amb. 1: 104–115. *t. 30–34.* 1741.

Sitodium [Banks & Solander ex] Parkinson, Jour. Voy. Endeavour, 45. 1773, nomen subnudum.

Rademachia Thunb. Vet. Akad. Handl. Stockholm 37: 251. 1776; Houttuyn, Nat. Hist. II. Pl. 11: 446. 1779. TYPE SPECIES: *Rademachia incisa* Thunb. (= *Artocarpus communis* J. R. & G. Forster).

Sitodium [Banks & Solander ex] Thunb. Philos. Trans. Roy. Soc. London 69: 465. 1779, nomen illegitimum.

Sitodium Banks [& Solander] ex Gaertn. Fruct. 1: 344. *t. 71, 72.* 1788, nomen illegitimum.

Polyphema Lour. Fl. Cochinch. 546. 1790. TYPE SPECIES: *Polyphema jaca* Lour. (= *Artocarpus heterophyllus* Lamarck).

Saccus O. Kuntze, Rev. Gen. 633. 1891, nomen illegitimum.

Small to large trees. *Leaves* spirally arranged (subg. *Artocarpus*) or alternate and distichous (subg. *Pseudojaca*), simple and entire to pinnatifid, or pinnate (*A. anisophyllus*), penninerved (basally trinerved in *A. altissimus*), thinly to thickly coriaceous, glabrous to pubescent or hispid; epidermal gland-hairs superficial to deeply immersed, heads globose to

flattened and peltate, 1–16-celled; spongy mesophyll long-armed and usually very loose (subg. *Artocarpus*), with ellipsoid to globose resin-cells (except in *A. integer* and *A. heterophyllus*), or compact, lacking resin-cells (subg. *Pseudojaca*); juvenile leaves entire to pinnatifid, or pinnate (*A. tamaran*), or with the lamina reduced to a sinuous wing along the midrib. *Stipules* paired, large, intrapetiolar, amplexicaul, scars annulate (subg. *Artocarpus*) or small, non-amplexicaul, scars lateral or intrapetiolar (subg. *Pseudojaca*).

Inflorescences unisexual, capitate, head cylindric to clavate, obovoid, ellipsoid or globose, lobed (in syncarp) or not, pedunculate (rarely subsessile), solitary or paired in leaf-axils, rarely borne on short shoots on older wood (subg. *Pseudojaca*) or rami- or cauliflorous (*A. integer*, *A. heterophyllus*); numerous flowers compactly covering surface, the perianths enclosing a single ovary or stamen, mixed with abundant stalked, peltate, varying to clavate or spathulate interfloral bracts, these often caducous from syncarp, or in some species entirely lacking, or in one (*A. styracifolius*) enlarging to form flexuous processes on syncarp; involucre absent (top of peduncle forming an annulus in *A. heterophyllus*). *At anthesis*: *male head* with perianths tubular and bilobed or perforate above, to 2–4-partite, stamens short- to long-exserted, anther-cells globose to oblong; *female head* with perianths tubular, thin-walled below and enclosing ovary, thick-walled above with a narrow lumen containing the style, partially or completely (in some species of subg. *Pseudojaca*) fused with one another to form syncarp; partial fusion occurring only between distal thick-walled region of perianths to form an external wall, with proximal thin-walled region remaining free; perianths completely fused above to form a smooth or areolate surface with the styles exserted through perforations, or the apices free, forming cylindric, conical, umbonate or truncate, rigid or flexuous processes on surface, all with styles exserted from their tips, or some processes sterile (in some species of subg. *Artocarpus*), solid, elongate and projecting beyond the rest (some of these species also with sterile, solid, elongate flowers in the male head); ovary unilocular, the style apical to lateral, simple or bifid (branches sometimes very unequal), the ovule subapical to lateral. *Mature syncarp* formed by the enlargement of the entire female head, with one to many flowers forming fruit; proximal portions of fruiting perianths, if free, either becoming fleshy or not, the remaining perianths elongated and ribbon-like; mature ovary thin-walled to fleshy or horny, or developing an indurated endocarp freed by decay of rest of wall, the style apical to sub-basal, the seed large, attached subapically to sub-basally, testa membranous to pergamaceous, endosperm none, the embryo straight, orientation longitudinal or oblique, cotyledons equal or not, appressed faces at an angle of 0–90° to median plane of ovary, radicle and plumule small to minute, apical or lateral; germination hypogeal.

DISTRIBUTION: Ceylon, India, Pakistan, Burma, Siam, Indochina, southern China, Malaysia, Solomon Islands; two species (*A. communis*, *A. heterophyllus*) cultivated throughout the tropics.

HISTORY OF THE GENUS AND NOMENCLATURE OF BREADFRUIT, CHEMPEDAK AND JACK

The genus *Artocarpus* is represented by indigenous species in an area extending from India and Ceylon to southern China, and through Malaysia to the Solomon Islands, while two species — the Breadfruit and the Jack — are now cultivated throughout the tropics. That it was, nevertheless, unknown to Linnaeus is somewhat surprising in view of the distinctiveness and economic importance of some of the species and the excellent descriptions which they had received from earlier authors.

The Jack was probably briefly mentioned by Theophrastus in about 300 B.C. as occurring in India and it figured more extensively in many later travellers' tales. The Breadfruit was first mentioned at the end of the sixteenth century by voyagers in the Pacific, where it was already widespread and of great importance to the Polynesians; it was recorded as far west as Java in 1642 and had become circumtropical in cultivation at least by the close of the eighteenth century.

Pre-Linnaean botanical descriptions. Among early botanical writers, Rheede described in 1682 both the Jack, which was already cultivated through most of tropical Asia and Malaysia, and a species of the Western Ghats, *Artocarpus hirsutus*, under the vernacular names *Tsjaka-maram* and *Ansjeli* (Hort. Ind. Malab. 3: 17, 25. *t. 26–28, 32*). At about the same time Rumphius prepared very full descriptions of the Jack and the Chempedak (then, as now, almost restricted to and less commonly cultivated in Malaysia) as *Saccus arboreus major* and *S. a. minor*; of the seedless and seeded forms of the Breadfruit and an allied wild species of the Moluccas as *Soccus* [sic] *lanosus*, *S. granosus* and *S. silvestris*, respectively; and, finally, of another Malaysian species, *Artocarpus fretissii*, as *Metrosideros spuria* (Herb. Amb. 1: 104–115. *t. 30–34*. 1741, 3: 26. *t. 13*. 1743). These are the most important pre-Linnaean botanical references to members of the genus, but several species from the Philippines were listed under their vernacular names, with brief descriptions, by J. G. Kamel (in Ray, Hist. Pl. 3, App. 51, 52. 1704). No attempt was made to identify Rumphius' plants by Linnaeus in 1754 (Herb. Amb. [resp. O. Stickman]), except for *Metrosideros spuria*, which he wrongly equated with *Ochna jabotapita* L. Nor did Burman provide any further identifications in his indices to the "Herbarium Amboinense" published in 1755 and 1769.

In 1891 Kuntze held that the generic name *Saccus* had been validly published by Rumphius and, accordingly, he made many new combinations under it. These are illegitimate, however, and are omitted from the synonymy of the various species.

Post-Linnaean botanical descriptions. Once the genus had become known to post-Linnaean botanists, it was described, within about twenty years, under four different generic names, *Sitodium* (1773, 1779 and 1788), *Artocarpus* (1776), *Rademachia* (1776) and *Polyphema* (1790), but the

name *Artocarpus* has been in continuous and undisputed use until doubt recently arose as to its priority, resulting in its conservation over *Sitodium* (1773). A review of the facts concerning these various publications follows, in which an attempt is made to determine their status and hence to establish whether the conservation of *Artocarpus* was necessary. This review is extended to cover the nomenclature of the Breadfruit, Chempedak and Jack — the only species in which any serious problems have arisen — since this will involve the addition of only two items to the material literature and will avoid later repetition, as well as provide a detailed picture of the early botanical history of the genus. Except for the earliest description of *Sitodium* and Houttuyn's publication of *Rademachia* the discussion will be largely based on the two papers published by Corner in 1939, although all the references have been carefully re-examined. For each name the Rumphian and post-Linnaean synonyms cited will be given and the factors taken into consideration in deciding its status will be clearly stated.

SITODIUM, ARTOCARPUS AND RADEMACHIA. The Breadfruit was the first species of the genus of which a description was published under a Linnaean binomial. This was done, under the name *Sitodium-altile* [sic], by Stanfield Parkinson in 1773 in his edition of "A Journal of a Voyage to the South Seas, in His Majesty's Ship, The Endeavour," which was written by his brother Sydney, who accompanied Sir Joseph Banks and Dr. Solander as an artist on Cook's first voyage around the world (1768–1771) but died on the way home from Batavia. In this was included a series of notes on plants seen in Tahiti, to most of which were appended, without acknowledgement, hyphenated "Latin names" corresponding to the binomials in Solander's manuscript "Primitiae Florae Insularum Oceani Pacifici, . . ." now in the British Museum (Natural History), London. This journal had been generally overlooked until Fosberg drew attention to it in 1939 (Am. Jour. Bot. 26: 229–231) and stated that Parkinson's description would necessitate the conservation of *Artocarpus* over *Sitodium*, which was finally achieved on these grounds in 1955 (Taxon 4: 162. 1955). In anticipation of this action the new combination *Artocarpus altilis* (Parkinson) Fosberg was published by him in 1941 (Jour. Wash. Acad. Sci. 31: 95) as the correct name for the Breadfruit.

However, Sydney Parkinson's notes are totally unscientific and mostly very brief; he was apparently quite unaware of the significance of his action in using those of the binomials that were new, as was his brother in publishing them, and few of them have any claim at all to valid publication. The account of the Breadfruit happens to be rather longer than the others but is merely a general description of which the "botanical" part is given below.

E ooroo *Sitodium-altile.*

. . . This tree grows to between thirty and forty feet high, has large palmated leaves, of a deep grass-green on the upper-side, but paler on the under; and bears male and female flowers, which come out single at the bottom or joint of each leaf. The male flower fades and drops off; the female, or cluster of females,

swell and yield the fruit, which often weighs three or four pounds, and is as big as a person's head when full grown. It is of a green colour; the rind is divided into a number of polygonal sections; the general shape a little longer than round, and white on the inside, with a pretty large core. The fruit, as well as the whole plant, is full of a white clammy juice, which issues plentifully from any part that is cut: . . .

In order for this description to be validly published it would have to be adequate as a "generico-specific" description, as was pointed out by Dandy and Exell *in litt.*, cited by Merrill (The Botany of Cook's Voyages. Chron. Bot. 14: 330. 1954) in the course of a detailed discussion of Parkinson's journal. Merrill's view that the description is not valid seems fully justified, the more so if the circumstances of publication are taken into consideration. This question must, however, always remain a matter of opinion and, since it has now been settled, for any who feel that they must recognize the validity of Parkinson's description, by conservation, its chief importance is in determining the specific epithet to be applied to the Breadfruit. The source of the generic name *Sitodium* is nowhere directly indicated in the literature of the eighteenth century, but it is now generally recognized that the authors should be cited as [Banks & Solander ex] (or [Solander ex]) Parkinson, etc.

A botanical description of the Breadfruit was published in 1776 under the name *Artocarpus communis*, with *Soccus* [*lanosus* and *granosus*] in synonymy, by J. R. & G. Forster, who were the botanists on Cook's second voyage around the world (1772–1775) (the generic name being derived from the Greek *artos*, bread, and *karpos*, fruit). In the same year another description of the Breadfruit, together with one of the Chempedak, was published under the generic name *Rademachia*, with the specific epithets *incisa* (synonyms: *Soccus lanosus*, *S. granosus* and *S. silvestris*) and *integra* (synonyms: *Saccus arboreus major* and *S. a. minor*), respectively, by C. P. Thunberg in a paper dated Batavia, d.15 Junii 1775. The name was given in honour of Herr Radermacher, then "Baillou" of Batavia, from whom Thunberg received much assistance, especially later, when he returned from Japan. It has not been possible to determine which of these two names was published first. The preface to the Forsters' "Characteres Generum Plantarum" was dated November 1775, and there is no reason to doubt that the title-page is correct in giving the date as 1776, but no more precise evidence is available. Thunberg's description was published in the July–September issue of the Kongl. Vetenskaps Acadamiens Handlingar for 1776, but Merrill (l.c., 359) stated that Hultén had been unable to find any record of the date of publication in Stockholm. Although it seems likely that *Artocarpus* was actually published before *Rademachia*, unless this can be established, the first person to choose between the two names must be followed. It has always been assumed that this choice was made by Linnaeus *filius* in 1781 in his "Supplementum Plantarum" when he used the name *Artocarpus*, combining both generic descriptions, though without giving *Rademachia* as a synonym. He recognized two species, *A. incisus* and *A. integrifolia* [sic], basing his descriptions on those of Thun-

berg and citing his names, and the same Rumphian names, but not *A. communis*, in synonymy.

It has, however, been overlooked that in 1779 Houttuyn had republished, in an account entitled "Beschryving van den Oostindischen Broodboom" which he included in his "Natuurlyke Historie," Thunberg's description of *Rademachia* (from a manuscript in Thunberg's hand sent to him by Radermacher) and had chosen his name to replace that of the Forsters on the grounds that the description was more complete, in that the formation of seeds was mentioned, whereas the description of *Artocarpus* was based solely on the seedless form of the Breadfruit. Houttuyn cited *"Artocarpus"* in synonymy under *Rademachia incisa*, in addition to the Rumphian names, and this would certainly have necessitated the conservation of *Artocarpus* over *Rademachia*, but for the fact that he did not know of the earlier publication of Thunberg's name in Sweden and hence was, giving his state of knowledge and intentions priority over the fortuitous circumstances, acting in contravention of present-day rules of nomenclature. Houttuyn's specific descriptions were based, in part at least, on material sent to him by Radermacher and, from his account of *Rademachia integra*, it seems that he had received the foliage of the Chempedak, but the fruit of the Jack. He also described very briefly a third species, *R. rotunda* (*Artocarpus rotunda* (Houtt.) Panzer, Pflanzensyst. 10: 380. 1783; in a translated and amplified version of Houttuyn's paper), which it has not been possible to identify, although Merrill (Jour. Arnold Arb. 19: 331. 1938) reduced *Artocarpus rigidus* to synonymy under Panzer's name. *Rademachia rotunda* will therefore be discussed further under that species. (Merrill did not comment on Houttuyn's reduction of *Artocarpus*.)

The Breadfruit. In determining the correct name for the Breadfruit, if the specific epithet *altilis* is rejected as invalidly published and Houttuyn's action is ruled illegitimate, it remains to consider whether the choice made by Linnaeus *filius* in forming the name *Artocarpus incisus* for this plant is legitimate. The use of the name *Artocarpus communis* in its place was first formally recommended by Richter in 1894 (Bot. Centralbl. 60: 169) on the grounds of its priority, and he was followed by various authors, including Merrill. The question was next fully discussed by Corner in 1939 (Gard. Bull. Singapore 10: 280) who concluded that, as the Rules then stood, Linnaeus *filius* was perfectly free, in making the choice between two simultaneously published names, to take the generic name from one genus and the specific epithet from the other (although he had chosen *incisus* over *communis* only by implication, this is all that is now required). According to Article 57 of the International Code of Botanical Nomenclature, 1956, this is still true; there is nothing to indicate that the choice of generic name determines the specific epithet, where both are simultaneously published. Therefore, if the generic names and specific epithets are considered *independently*, the argument is valid and it is only after much deliberation that the decision has been made to reject it in the interests of stability of nomenclature and in order to follow the general principles of the Rules.

In the present example, Article 57 is in conflict with Principles III and IV, especially the latter: "Each taxonomic group can bear only one correct name [which for a species is a binary combination; see Art. 23], the earliest that is in accordance with the Rules, ..." *Artocarpus* became the correct generic name through the choice made by Linnaeus *filius*; thus the earliest *combination* based on the Breadfruit that is in accordance with the Rules is *Artocarpus communis* (1776). The name *Artocarpus incisus* (1781) is also legitimate at present (apparently it is not in conflict with Article 11), but, if any change were considered necessary in Article 57 in order to deal with this unusual problem, the Article would undoubtedly be brought into line with the Principles.

St. John (Pacific Sci. 2: 109. 1948), in the only other detailed consideration of the nomenclature of the Breadfruit, concluded that the name *Artocarpus incisus* should be used, following both Article 57 (then no. 56) and established custom. However, there has been uncertainty as to the correct name of the Breadfruit for over fifty years. *Artocarpus communis* has been gaining gradually in acceptance over *A. incisus* and is now perhaps more widely used. With the addition of *Artocarpus altilis* as a third possibility, the situation has become more confused during the last two decades. It is evident that "established custom" cannot provide a stable solution to the problem. Moreover, in view of the long-standing uncertainty, any argument based on custom has lost much of its force in this particular instance, although the general desirability of following custom, where there is genuine doubt as to the consequences of the Rules, is not questioned. It is regretted that the name *Artocarpus incisus* was used in the first paper of this series.

The Chempedak. Turning now to the second species described by Thunberg and Linnaeus *filius*, this was until recently erroneously identified as the Jack, to which the name *Artocarpus integrifolia* was universally applied from the beginning of the nineteenth century until it was partially replaced in the literature by the legitimate combination *A. integer*. This was made by Merrill in 1917 (as *A. integra*, Interpr. Rumph. Herb. Amb. 190), to replace Linnaeus *filius*' superfluous name, and was used by him in his consideration of Rumphian names in the same sense, i.e., as the correct name for *Saccus arboreus major*.

In 1939, however, Corner demonstrated conclusively, in a paper on the distinguishing characters and nomenclature of the Jack and the Chempedak (Gard. Bull. Singapore 10: 56–81. *t. 1, 2*), that Thunberg's description had been based solely on the Chempedak. Although the latter had cited both *Saccus arboreus major* and *S. a. minor* as synonyms, and had given the Malay name of the tree as *Tjampeda*, but that of the fruit as *Nanca* (the Malay name for the Jack) and thus had, apparently, attributed the fruit of the Jack to the foliage of the Chempedak (as is also indicated by the material received by Houttuyn), only the vegetative parts were included in his description (with a note in Swedish that the roots, stems, branches and flowers were as in the preceding species [*Rademachia incisa*]). From the shape and colour of the leaf and the indumentum of rigid, patent

hairs on the lower surface, twigs and peduncles, Corner showed that the description could refer only to the Chempedak (the Jack being glabrous), so that, in spite of the confusion in the Malayan and Rumphian names, the application of Thunberg's name is unambiguous. The distribution was given by Thunberg as Java, around Batavia, and (from Rumphius) Amboina and other places. Corner stated that Professor Svedelius had examined the type specimen at Uppsala and had found that it consisted of material of the Chempedak agreeing with Thunberg's description and including male inflorescences without the annulus at the base of the head that is found only in the Jack. Mixed with it was material of the Jack (see photographs in Corner, l.c.) which, from the note on the back of the sheet, "e Ceylona Thunberg," had probably been collected in Ceylon, where the Chempedak does not occur (presumably on Thunberg's visit there in 1777–78 on the way back from Batavia). Professor Svedelius thought that by an error the two plants of different origin had been put on the same sheet when Thunberg's collections were mounted some years later. This was confirmed by the discovery, in the course of the present revision, of a sheet in the Rijksherbarium, Leiden, bearing only the Chempedak and labelled by Thunberg "RADEMACHIA integra Thunb.," which was presumably part of the material sent to Houttuyn.

THE JACK. Thunberg showed that he had completely failed to perceive any difference between the Jack and the Chempedak in a paper published in 1779 with the title "Sitodium *incisum et macrocarpon, ususque fructuum qui exinde nascuntur, descripta a* Carolo Petro Thunberg, *M.D.*," in which he altered the generic name *Rademachia* (now spelling it more correctly as *Radermachia*) to *Sitodium* without giving either his reasons or any source for the name, although he had presumably obtained it from Banks, who communicated the paper to the Royal Society of London. The generic description (with *Soccus, Saccus, Radermachia,* and *Artocarpus* as synonyms) had only minor changes in wording and *Rademachia incisa* and *R. integra* were cited (in addition to the previous Rumphian names) under the two species, respectively, in synonymy. Therefore, although they are validly published here, the generic name *Sitodium* and the specific epithet *macrocarpon* must be rejected as nomenclaturally superfluous and thus illegitimate. Under *Sitodium macrocarpon*, Thunberg added to his previous Latin description of the Chempedak an account of the juvenile leaves and the fruit of the Jack (with a popular account of its uses in Ceylon, including recipes!). His paper renders illegitimate as a later homonyn Gaertner's independent publication in 1788 of the generic name *Sitodium*, attributed by him to Banks. This was based on another description of the fruit of the Jack under the name *Sitodium cauliflorum*, but, as stated by Corner, the latter must also be regarded as a superfluous name for the Chempedak, since the author's intention, as indicated by the indirect citation of *Artocarpus integrifolia* ("*Artocarpus foliis integris.* LINN. [ed. Murray,] *syst. veg. 838.*" [1784]) together with *Soccus arboreus* [sic] in synonymy, was to replace the earlier name, and this intention must be given

priority over the description and plates. Gaertner was the only author previous to Corner (l.c.) to describe and draw the female perianths (called by him "baccae partiales") as free below, though fused above.

Lamarck, in 1789, was the first post-Linnaean author to make a distinction between the Jack and the Chempedak, when he described in his "Encyclopédie Méthodique" three new species based on the Jack: *Artocarpus heterophyllus* (as *A. heterophylla*), with *Saccus arboreus major* as a synonym; *A. jaca*, which he recognized as close to the former, with Rheede's *Tsjaka-maram* among its synonyms; and *A. philippensis*. Under *Artocarpus jaca* he recognized a variety "*β. Eadem ramulis petiolis foliisque subhirsutis*," giving *Saccus arboreus minor*, *Artocarpus integrifolia* and *Rademachia integra* as synonyms. Unfortunately Lamarck's "illegitimate" action, while making this perfectly correct distinction, in thus subordinating the variety based on the earlier names and descriptions applicable to the Chempedak (of which he had seen no specimens) under his new species must, following Corner, make *Artocarpus jaca* yet another superfluous name for the Chempedak. The latter therefore, since no previous effective choice had been made between the two other simultaneously published names (for both of which Lamarck had mentioned the characteristic annulus at the base of the inflorescence head), took *A. heterophyllus* as the more appropriate, so that this becomes the correct name for the Jack. Examination in 1955 of the type material of the three species in the herbaria of Lamarck and de Jussieu (the latter including that of Commerson) at the Muséum National d'Histoire Naturelle, Paris, has confirmed that it consists solely of specimens of the Jack and that the species were based on somewhat marked differences in the leaves. Lamarck also included *Artocarpus incisus* (synonyms: *Soccus lanosus*, *S. granosus*, *Rademachia incisa*, "*Artocarpus* Forst.") in his account of the genus and described a fourth new species, *A. hirsutus* (as *A. hirsuta*), which he based entirely on Rheede's *Ansjeli*.

In spite of this distinction between the Chempedak and the Jack, the transference of the name *Artocarpus integrifolia* (with *Rademachia integra*) from the former to the latter was effectively achieved by Willdenow in 1805 in his edition of the "Species Plantarum" (the next work in which the genus was treated at all fully). He then "corrected" Lamarck's nomenclature, changing the name of his second species based on the Jack from *Artocarpus jaca* to *A. integrifolia*. He cited *A. jaca*, together with *Rademachia integra* and *Tsjaca-maram*, in synonymy, and recognized two varieties, "*β.* ramulis petiolis, foliisque subtus hirsutis" with *Saccus arboreus minor* as the only synonym, and "*γ.* foliis indivisis trilobisve" with *Artocarpus heterophylla* and *Saccus arboreus major* as synonyms.

Polyphema. The description by Loureiro in 1790 of a new genus *Polyphema* to take the place of Linnaeus *filius'* *Artocarpus integrifolia* was due to a complete misunderstanding of the latter's generic description, which led Loureiro to suppose that it could only correspond to the first species, *Artocarpus incisus*, not seen by him, and to make several distinc-

tions between it and the plants he was studying which he felt justified their segregation as a new genus. Under this he described the Jack as *Polyphema jaca*, with *Saccus arboreus major* as a synonym, and the Chempedak as *P. champeden*, with *Saccus arboreus minor* as a synonym, and thus correctly separated the elements confused in *A. integrifolia* (though only in the synonymy). His description of the Jack appears to be entirely original (the type is in the British Museum (Natural History), London), but that of the Chempedak is largely based on Rumphius' account and it is doubtful whether he had ever seen a specimen. The plant is not found in Indochina in spite of his statement that it occurs in high woods there, and he may have been referring to a native species which he also used in making the description; the precise derivation of his account will be discussed further under *Artocarpus integer*.

Willdenow did not mention Loureiro's generic name, but in 1807 Sprengel made it the basis of an illegitimate name for the Chempedak, *Artocarpus polyphema*, under which this plant has been most widely known in the literature, although it was corrected to *A. champeden* in 1812 (by Stokes, Bot. Mat. Med. 4: 330; but universally ascribed to Sprengel, Syst. Veg. 3: 804. 1826).

HISTORY OF THE GENUS FROM 1807. A few other species were described in *Artocarpus*, but the first major contribution to the taxonomy of the genus was made by Trécul in 1847 in his paper on the Moraceae: Artocarpoideae and Conocephaloideae entitled "Mémoire sur la Famille des Artocarpées." He based his account mainly on the material then in the Muséum National d'Histoire Naturelle in Paris, and distinguished fifteen species, of which seven were new. In view of his limited material his work was very accurate and it is the only complete revision of the genus previously undertaken. He divided *Artocarpus* into two subgenera, *Jaca* (= subg. *Artocarpus*) ["*Perigonium* masculum diphyllum, foliolis plus minusve inter se cohaerentibus; *stipulae* duae oppositae, amplexicaules, altera marginibus alteram tegens; *folia* alterna"] and *Pseudojaca* ["*Perigonium* masculum tetra- rarissime triphyllum; *stipulae* 2 minimae, axillares vel sublaterales, non oppositae, nec amplexicaules; *folia* disticha"]. These subdivisions have been found to be well marked, although, as was pointed out by King (1889), the distinction based on the male perianth is not valid, since this is more variable within subgenus *Pseudojaca* than Trécul realized, even within the species studied by him. His use of the term opposite with respect to the stipules was a source of confusion to King, as shown by Renner (1907), since he restricted it to stipules having their midlines 180° apart.

In the years 1861 and 1867, Miquel published altogether 16 new species and combinations in *Artocarpus* (in addition to four that had appeared earlier), but many of the descriptions were based on poor material and it has only been possible to identify them by studying the types. More than one species was described under several different names and, although Miquel recognized Trécul's subgenera, he included in subg. *Artocarpus* a

species of *Sloetia* (Moroideae) and in subg. *Pseudojaca* one species (*A. limpato*) later transferred to *Prainea* and three which have been reduced to *Parartocarpus venenosus* (Zoll. et Mor.) Becc. (itself originally described as a species of *Artocarpus* in 1845).

The next important paper on the genus was King's monograph of 1889, "The species of *Artocarpus* indigenous to British India," in which he described seventeen species (seven of them and two varieties as new) known to him as native in India, Ceylon, Burma and Malaya. They were usually correctly defined (except for the two varieties), but, owing to his inability to study the types of Miquel and other authors, several of King's names must be replaced by earlier ones. He rejected Trécul's subgenera and arranged the species in two groups, in the first of which [the distal portions of] the "anthocarps" [1] were only partially united with each other so that the syncarp was spiny or tuberculate, while in the second they were completely united and the surface of the syncarp was smooth. Except for two new species included at the beginning of his first group (*Artocarpus forbesii* and *A. bracteata*) the subdivision does, however, correspond to Trécul's subgenera; this distinction between them happens to be fairly satisfactory in the species which King was considering, although, as was pointed out in the introductory paper, it does not hold for the entire genus. These two species should have been referred to *Parartocarpus* (in which the leaves are spirally arranged with non-amplexicaul stipules and the inflorescences are involucrate) and they represent the two other species which will be recognized in the genus. King did not mention *Parartocarpus*, and, although the description had been published in 1875, it may not have been available to him. The syncarps of these two species closely resemble those of some species of *Artocarpus* and King mistook the solid spinous process on the surface (the nature of which was discussed in the introductory paper) for tubular, perforate perianth apices. He did not consider leaf arrangement (explicitly at least), although his two groups differed in this respect also, and he rejected Trécul's perianth and stipular characters. The rejection of the stipular character was due to a double confusion: as already noted, King failed to comprehend Trécul's peculiar use of the term opposite; it has further been found in this study that he assigned a sterile specimen of *Artocarpus rigidus* to his *A. bracteata*, which caused him to describe the shoot as annulate, as it was in all the other species of his first group except *A. forbesii*, so that the stipular character would not give a "natural" classification, whereas the syncarp character apparently would. He considered that whether or not the stipules were amplexicaul depended merely on their size, and evidently attached no special significance to the occurrence of a basal involucre, which he observed only in *A. bracteata*.

In 1902 Beccari described nine new species and one new variety of *Artocarpus* from Borneo and New Guinea in an appendix to his "Nelle Foreste

[1] I.e., the female perianths; this term can, strictly, be applied only to those perianths enclosing mature seeds. It has not been used, since it would merely complicate the specific descriptions.

di Borneo," in which he also considered the characters in which *Prainea* and *Parartocarpus* differ from *Artocarpus*, though without fully clarifying them (see under *Prainea* above and *Parartocarpus* to follow), and removed King's two wrongly assigned species to *Parartocarpus*.

Finally, Renner, in a paper entitled "Beiträge zur Anatomie und Systematik der Artocarpeen und Conocephaleen, insbesondere der Gattung *Ficus*" published in 1907, discussed the systematy of the genera being studied, chiefly on the basis of their leaf anatomy, and, reinstating Trécul's subgenera, concluded that they, together with *Prainea*, should be treated as sections under *Artocarpus*. Renner's action in uniting *Prainea* with *Artocarpus* has been fully discussed in the introductory paper to this series and has been rejected, since the differences in leaf anatomy (and leaf arrangement) between the two subgenera (here maintained at this rank) could well have arisen by divergence from a common ancestor with the somewhat intermediate *Prainea*, whereas the unique syncarpium of *Artocarpus* indicates a close taxonomic relationship between the subgenera and contrasts markedly with the free female perianths of *Prainea*. Later authors have ignored both Renner's reduction of *Prainea* and Trécul's subgenera. Renner listed the anatomical characters for each of the species of *Artocarpus* available to him, citing the specimen(s) he had examined, but suggested no further taxonomic innovations, although his arrangement of the species follows a fairly "natural" order. The examination of leaf anatomy has been repeated for each of the species here recognized and details of the microscopic epidermal gland-hairs and of the hypodermis, if present, are given for each of the species in subg. *Artocarpus*, since their characters are of value in establishing the series.

Two purely taxonomic treatments should perhaps be mentioned, namely, Elmer's "Synopsis of *Artocarpus*" treating 16 species of the Philippines (1909), and Gagnepain's account of the genus in the "Flore Générale de l'Indochine" (1928) for which he described eight new species in 1926, several of which must be reduced.

There should also be added here a note on a paper which has only recently come to my notice, on the structure of the jackfruit, by D. D. Sundararaj and K. Ramanujam, "Studies on the floral morphology of Jack, *Artocarpus heterophyllus* Lamk. (Syn.: *A. integrifolius*, L.f.)," S. Indian Hort. 1: 56–61. *figs. 1–12*. 1953. These authors have described and illustrated the structure of the jackfruit at anthesis and maturity, and have emphasized, as was done in the introductory paper to this series, that the perianths are free below but fused above, in this species leaving the apices free, so that they have recognized three regions in each perianth. They have also pointed out again that, as had been made clear by Corner (Gard. Bull. Singapore 10: 56–81. 1939), the true fruits are enclosed by the free fleshy lower portions of the fruiting perianths. They describe the syncarp as a false fruit. However, they do not seem to have examined any very young female heads, in which the perianths would presumably be entirely free (as in *A. rigidus*, described in the introductory paper). They also state positively, but without bringing forward any evidence, that the an-

nulus represents the involucral bract of the inflorescence, whereas Corner had noted (l.c., 62, 76) that he had been unable to discover its morphological nature, although it was probably comparable to the bracts in *Pararto-carpus*. This may well be the origin of the irregular row of bracts and the slight swelling of the top of the peduncle seen in some other species of *Artocarpus* but it is possible that the annulus represents a secondary enlargement of the latter.

Gender of Artocarpus. Although the International Code of Botanical Nomenclature now states that *Artocarpus* must be treated as a masculine noun, since the Greek masculine noun *karpos* has been further altered to the masculine form in Latinization (Recommendation 75A), the genus has been considered as feminine by almost all previous authors except Linnaeus *filius* (1781), Renner (1907) and Corner (1939, 1940). The original specific epithet in *Artocarpus* — *communis* — was ambiguous in this respect, while Linnaeus *filius* treated his first species as masculine — *A. incisus* — but the second as feminine — *A. integrifolia*. Renner pointed out that this error probably arose in type-setting, since both the other species on the same page had feminine terminations, and he supposed that it had been perpetuated through the custom in Latin of treating all names of trees as feminine. In this revision only the original form in which a given name was published is indicated, if different from that now accepted (in addition to significant typographical errors).

CLASSIFICATION OF THE GENUS

The two subgenera of *Artocarpus*, established by Trécul in 1847, are here recognized on grounds which have already been fully discussed in the introductory paper in which they were also keyed out with the genera (p. 26, above). The characters distinguishing them, of which the vegetative are of more practical importance than the reproductive, may be summarized as follows: in subg. *Artocarpus* the leaves are spirally arranged with large, amplexicaul stipules leaving annulate scars and they have a long-armed, usually very loose spongy mesophyll with ellipsoid to globose resin-cells, and epidermal gland-hairs with a 4–16-celled head, whereas in subg. *Pseudojaca* the leaves are alternate and distichous with small non-amplexicaul stipules leaving lateral or partially intrapetiolar scars, the mesophyll is compact, and the heads of the gland-hairs are usually unicellular. The syncarp in subg. *Pseudojaca* is globose or somewhat lobed with a fleshy, smooth or papillate surface, while in subg. *Artocarpus* both shape and surface are variable, though the syncarp usually bears distinct indurated or fleshy processes, or, where it is smooth or nearly so, it is ellipsoid to cylindric.

While the species in this genus are, on the whole, distinct and readily separable, this is not always the case with the subdivisions between the level of the subgenus and the species. There is also a marked contrast

in the range of variation exhibited within the two subgenera and this is reflected in the classification here suggested for the species within them. In subgenus *Artocarpus* there is a wide range of variation — within the fairly strict limits imposed by the structure — in the syncarps (especially in the shape, length, consistency and indumentum of the processes) and the species can be recognized on the differences in these alone, although they are supported by more or less marked differences in the male inflorescences (in shape, size and surface, and in peduncle indumentum and length) and in the shoot (in indumentum and leaf size and shape). The pattern of variation warrants the creation of two sections with two and four series, respectively, the basis for which will be discussed below.

In subgenus *Pseudojaca*, on the other hand, while two sections will also be created, one is for an anomalous species, *Artocarpus altissimus*, and the other presents little variation between the species. The inflorescences are so reduced that the entire male and female heads provide the unit of variation in establishing the species. The heads of different species vary in size and shape, in the length and indumentum of the peduncle, and, in the female head, in the appearance of the surface at anthesis and maturity, its indumentum, the degree of exsertion of the styles, and whether or not the interfloral bracts persist or lobing develops. There are also vegetative differences between the species — in shape, size, prominence of venation, petiole length and indumentum of the leaf — but, while most species can, with practice, be identified when sterile, the differences are often not readily definable. As might be expected where there are limited possibilities for variation, parallel evolution has occurred, especially in the vegetative characters, and the species may only be definable by using a combination of characters. The only discontinuous "morphological" variation occurring in this section is in the shape of the interfloral bracts, which is used to separate three species as one series of limited geographical distribution, leaving the remainder as a large group which is probably best treated as a single series. Although subsidiary groups can be recognized within the latter, the definitions necessary for these are somewhat complex, and there are also several species showing reticulate relationships, and a few of which the alliances are doubtful.

In the keys to both subgenera proportions have been used — length to breadth of inflorescence head in subg. *Artocarpus*, and length of head to length of peduncle in subg. *Pseudojaca*. These recognize and utilize characteristic differences between species groups in the shape of the head or in the relative length of head and peduncle. These differences hold, with a few exceptions, for both male and female inflorescences, thus making possible the construction of a "natural" key which can be used (at this dichotomy at least) at any stage in the development of the inflorescence, since the relationships remain fairly constant throughout its growth. The use of these ratios also allows for the considerable variation in size, rather than shape, which may occur in the inflorescences, depending largely on the part of the plant on which they are borne. There are some species, especially in subg. *Pseudojaca*, where these relationships do not

always hold, but they are relatively few in number and have been allowed for as far as possible.

ECOLOGICAL AND BIOLOGICAL NOTES

The species of *Artocarpus*, except for a few belonging to subg. *Pseudojaca*, are large trees of the high forest and are mainly restricted to evergreen forest in the tropical everwet zone or in areas with a relatively mild monsoon climate. They are usually found below an altitude of 3000 ft., though several species may occur up to 5000 ft. One species, *Artocarpus communis*, is abundant in swamp forest in New Guinea, and others are recorded from swampy areas or from the banks of streams. The majority of the species in everwet forest are themselves evergreen, although they may, especially in subg. *Pseudojaca*, show marked flushes of new growth, but *Artocarpus dadah* is deciduous. Of the species restricted to regions with monsoon climate some, including *A. lakoocha*, are deciduous, but others, such as *A. gomezianus*, are evergreen. The latter (as ssp. *gomezianus*) is the only entity within the genus to show a marked climatic discontinuity — between Lower Burma and Siam, and central and eastern Java. *Artocarpus lakoocha*, which is the most wide-ranging species on the continent of Asia, is also the most tolerant of cool temperatures and low rainfall, although it is damaged by frost.

In considering biological aspects of the variation in growth habit and in the syncarp in this genus several more or less parallel trends may be distinguished. The first tendency is shown in the arrangement of the leaves, which in subg. *Artocarpus* are borne spirally on usually ascending twigs, whereas the ultimate shoots in subg. *Pseudojaca*, with their alternate and distichous leaves form more or less applanate sprays of foliage. Associated with the latter habit is a general reduction in massiveness, but within each subgenus there are also tendencies to reduction in the size of parts, culminating in subg. *Artocarpus* in *A. kemando*, and in subg. *Pseudojaca* in *A. styracifolius*.

There is in subgenus *Artocarpus* considerable variation in the form of the adult leaves, which are pinnate in *A. anisophyllus* (though unusual in not disarticulating when they fall) and pinnatifid in *A. communis* and its allies, all these species having very stout twigs. In the saplings of several species the leaves are very large and highly dissected (twice or thrice pinnatifid and to six feet in length in *A. elasticus*). Members of this subgenus were mentioned by Corner in his exposition of the "Durian Theory" (Ann. Bot. II. 13: 367–414. 1949) as showing in their sapling and adult stages the transition from a "pachycaul" habit, with a sparingly branched trunk and large, compound leaves, to the modern "leptocaul" tree, with slender twigs and horizontal sprays of simple leaves. They were also noted as exhibiting the principle of "axial conformity" or correspondence between the massiveness of the axis and the size and complexity of its appendages, which may be extended through *A. anisophyllus* and *A. communis* to the most slenderly constructed species of both subgenera. Except in two cauliflorous species

of subg. *Artocarpus* (*A. integer* and *A. heterophyllus*) there is a general correspondence throughout the genus between the size of the twigs and leaves and that of the syncarps, which are borne with the male inflorescences among the foliage (although before they mature the subtending leaves may have fallen). A different trend was pointed out by Corner in *A. heterophyllus*, in which the twigs were slender with simple leaves, tending to form an applanate spray (cf. subg. *Pseudojaca*), while the enormous syncarp was borne on the trunk or large branches, a necessary development if the massive fruit was to be retained.

The syncarps within the genus also vary between two types of organization, namely, those in which each seed is surrounded by a pulpy perianth and the rest of the syncarp is more or less fibrous or indurated, and those in which the entire syncarp is soft and fleshy but the fruiting perianths are not markedly hypertrophied. The first type is best developed in the armoured syncarps of the first section of subgenus *Artocarpus* (which includes *A. rigidus*), and the second is found in the small, nearly smooth syncarps of *A. kemando* and its allies, and of subg. *Pseudojaca*. The remaining species in subg. *Artocarpus* have small to fairly large, moderately fleshy syncarps, usually with well developed firm, or fleshy and often flexuous processes on the surface. They lack (so far as evidence is available) conspicuously enlarged fruiting perianths, except in the very large syncarps of the two cauliflorous species. However, the perianths in *A. elasticus* and *A. sericicarpus* are apparently somewhat pulpy. In the species with an armoured syncarp and also in a number of species in subg. *Pseudojaca* the seeds are enclosed in more or less well differentiated horny endocarps which may become free by the decay of the rest of the pericarp, while in other species of subg. *Artocarpus* the entire pericarp is indurated. This protection is lacking in the cauliflorous species, but in *A. heterophyllus* there is a horny outer testa.

In spite of the varying nature of the attractive element in the syncarp of *Artocarpus* the mode of dispersal is much the same throughout the genus, which is primarily adapted for distribution by arboreal mammals, although the smaller fruits of subg. *Pseudojaca*, many of which are yellow, red or purple, may also be eaten by birds. (Troup (Silvicult. Ind. Trees 3: 884. 1921) records that the fruit of *A. lakoocha* is eaten by parrots and minahs, and also by monkeys.) The larger fruits in the genus, according to Ridley (The Dispersal of Plants. 1930), are bitten to pieces on the tree by monkeys, squirrels and civet-cats. He describes how the orange syncarps of *Artocarpus rigidus* (for which the English name is the Monkey Jack) are eaten in Malaya by a macaque monkey, which readily tears apart the spiny covering to reach the edible sweet orange pulp surrounding the seeds, and how as much fruit may be thrown away as is eaten. It is presumably by means of this wastage of portions of the fruit, which are let fall by the animals eating them, that the seeds are more widely dispersed, but they will, in any case, germinate in syncarps which fall to the ground from the tree. Ridley suggests that the enormous syncarps borne on the trunk in *A. integer* (and presumably also in *A. heterophyllus*) are eaten

by forest ungulates, such as wild cattle, pigs and elephants, which can easily reach them. It should be noted that the seeds in this genus have no period of dormancy, but germinate immediately, and that they are unable to withstand dessication.

The mode of pollination in *Artocarpus* is variable. Corner (Wayside Trees, 650. 1940) recorded that male heads in *A. heterophyllus*, *A. integer* and *A. dadah* had a sweet scent of honey and burnt sugar, attracting small flies and beetles, which were the pollinating agents, but that *A. rigidus*, *A. communis* and *A. elasticus* were apparently wind-pollinated, since the male heads had no scent, but gave off clouds of pollen when they were moved. Van der Pijl (Ann. Bogor. 1:79–82. 1953) studied pollination in *Artocarpus heterophyllus* and found that the anthers emerged over a period of some days and produced a sticky pollen. The flies bred on the decaying flower-heads which had fallen from the tree and thus established a brief symbiotic relationship with the plant during the period of anthesis.

Subgenus **Artocarpus**

Artocarpus subgenus *Jaca* Trécul, Ann. Sci. Nat. Bot. III. 8: 110. 1847.
Artocarpus section *Jaca* Renner, Bot. Jahrb. 39: 363. 1907.

Leaves spirally arranged, simple and entire to pinnatifid, or pinnate (*A. anisophyllus*); gland-hairs superficial to deeply sunken, heads 4–16-celled; spongy mesophyll long-armed and usually very loose, with ellipsoid to globose resin-cells (except in *A. integer* and *A. heterophyllus*). *Stipules* large, intra-petiolar, amplexicaul, scars annulate. *Inflorescences* with or without sterile, solid, elongate perianths. *Male head*, perianths tubular, shallowly (rarely deeply) 2(–3)-lobed above, or perforate. *Syncarp* globose or subglobose, covered by indurated processes, or ellipsoid to cylindric, varying subglobose, covered by firm or flexuous processes or less commonly areolate.

This subgenus is divided into two sections, *Duricarpus* and *Artocarpus*, based on the shape of the inflorescence heads and the presence or size of the interfloral bracts, on various characters of the syncarps, and, less certainly, on the mode of germination; but there are also three anomalous species which will be discussed below. The first section is a fairly homogeneous group of seven species, characterized primarily by the syncarp which has the surface armoured (whence its name) by the indurated free apices of the perianths. The free proximal region of those perianths that form seeds becomes fleshy, and encloses an ovary having a terminal style and developing a more or less clearly differentiated horny endocarp (becoming free by the decay of the rest of the pericarp in *A. anisophyllus* and *A. lanceifolius*). The embryo is symmetrical with a minute apical radicle and the appressed faces of the cotyledons at an angle of 30–90° to the median plane. The syncarp is globose or nearly so, and the male head varies from globose to cylindric or clavate, but is never more than three and one half (rarely four) times as long as broad. In both there

are conspicuous peltate interfloral bracts, but these are mostly lost from the syncarp at or before anthesis, although a few frequently persist. The mode of germination is known in several species and the first pair of leaves subsequent to the cotyledons is consistently opposite, though later leaves are spirally arranged. For comparison with the series of the next section, it may be noted that a hypodermis is present in the leaves of only two species and that it consists of cells which are elongate in surface view, while the gland-hairs have a globose, 4–16-celled head. On the basis of the leaf characters, together with a difference in the shape of the male heads, two species are separated as series *Laevifolii*, leaving the rest in series *Asperifolii*.

The second section, *Artocarpus*, is larger and more heterogeneous, but the species are united and are distinguished from sect. *Duricarpus* by their more or less elongate inflorescences, the absence or small size of the interfloral bracts and the fleshy syncarp with the fruiting perianths becoming markedly fleshy in only two species, and the mature ovaries with a lateral or sub-basal style and no clearly differentiated endocarp (so far as the internal structure is known; exceptions presented by the anomalous species will be noted below). The contrast in the shape of the inflorescences is more marked in the male head which is usually at least four times as long as broad (though as little as one and one half times in *A. heterophyllus*). The syncarp is, however, usually ellipsoid to cylindric and only rarely subglobose, and the surface is either covered by firm, or more or less fleshy and often flexuous processes of varying shape or, less commonly, merely areolate. Interfloral bracts are frequently entirely lacking and, when present, they are scattered and inconspicuous, with small heads to 0.2 mm. across. The position of the style, though variable, is always at least one third of the way down the ventral face of the ovary at maturity, and the radicle is likewise ventral, so that the long axis of the embryo is oblique. The appressed faces of the cotyledons lie either in the median plane of the ovary, in which case the embryo is usually symmetrical, or they are also more or less oblique, with the uppermost cotyledon frequently reduced in size. Details of germination are known for only four species (*A. communis*, *A. integer*, *A. heterophyllus* and *A. elasticus*) but the first leaves appear to be always spirally arranged, except, perhaps, in *A. communis*, and to be preceded by scale leaves.

The classification of the species within section *Artocarpus* has presented some problems, in addition to those originating in the three species that have been separated as anomalous. It has been concluded that four series should be recognized and these are based, as in sect. *Duricarpus*, primarily on characters of the leaves, namely the shape of the gland-hairs, and the presence or absence of a hypodermis and of resin-cells. However, with one exception, each is further distinguished by characters that are unique to it. Series *Rugosi*, with seven species, is readily distinguished by the anatomical characters of the leaves, which have a continuous hypodermis of isodiametric cells and gland-hairs with a depressed-globose, 4-celled head, and by the variously ridged surface of the male head, from which it receives its name.

In the other species of the section the surface of the male inflorescence is smooth (except occasionally in *A. integer*) and an irregular hypodermis is found only in some specimens of *A. blancoi*. Series *Incisifolii*, with six species, is also well distinguished by the flattened, peltate, 8(–16)-celled heads of the gland-hairs, the frequently pinnatifid adult leaves, the inflated hairs usually covering the syncarp processes and male perianth lobes, and the relatively large size of the anthers, which range from 0.3–1.5 mm. in length (in no other species of the subgenus do they exceed 0.5 mm.). The remaining series, *Cauliflori* and *Angusticarpi*, each with two species, have entire adult leaves with gland-hairs having a depressed-globose, 6–10-celled head and consistently slender twigs, as compared with series *Incisifolii*. Series *Cauliflori* is distinguished from series *Angusticarpi* (and all other species of the subgenus) by the very large syncarps borne on the branches and trunk, with markedly hypertrophied fleshy fruiting perianths, the absence of resin-cells from the leaves, and possibly also by the germination of the seed, in the course of which the two cotyledons separate to allow the emergence of the plumule. Although the cauliflorous syncarp of these species gives them a very distinctive appearance, the characters just listed do not appear to be of sufficient importance to justify separating this series from the rest in the section. Series *Angusticarpi* thus remains as an unspecialized, though generally reduced, group which does not show clear alliances with any other series. The appearance of the leaves is quite distinct from that of series *Cauliflori*, as may be seen from the key to the subgenus. The value of the syncarp in classifying this section, although considerable in distinguishing the species, is limited at the level of the series, since there has been parallel evolution in the development of sterile perianths forming elongate, solid processes on the surface in one or more species of all series except *Cauliflori*; in series *Incisifolii* and *Angusticarpi* there may also be similar perianths in the male inflorescence. While the embryos may well provide characters distinguishing the series — those of series *Incisifolii* have relatively well developed cotyledonary stalks and radicles and the entire pericarp wall is indurated — they are very variable from species to species and evidence is unfortunately insufficient to determine their taxonomic value. Details are given for each species in the section when available.

The validity of these groups is supported by their geographical distribution. Section *Duricarpus* and series *Rugosi* are both centred in western Malaysia (Malaya, Sumatra, Borneo, Java) and the former occurs northward to Sikkim and Indochina, and is perhaps represented by indigenous species in the Philippines, while the latter has one species reaching southern Tenasserim and Palawan, and another extending through the Philippines, to Celebes and the Moluccas. Series *Incisifolii*, on the other hand, has species in the Philippines, the Moluccas and New Guinea (and perhaps Melanesia if *Artocarpus communis* is indigenous there). The most widespread groups are series *Cauliflori* and *Angusticarpi*. The first has one species (*A. integer*) extending from western New Guinea to Malaya and reaching peninsular Burma and Siam, although it is absent from the Philippines,

and another (*A. heterophyllus*) perhaps indigenous in peninsular India. The second has one species in Malaya and Sumatra, and one with a distribution similar to that of *A. integer* but extending to the Nicobar Islands instead of north of the Malayan border.

On the basis, primarily, of the shape of the inflorescence heads, three species, which are otherwise anomalous in that each is, in various characters, intermediate between the sections, are placed at the end of sect. *Artocarpus*. Owing to this intermediacy and the fact that the structure of the mature syncarp is known in only one of them, they are not assigned to any of the series here established. Although a separate series should, perhaps, be created for each one of them, this is deferred, pending a more complete knowledge of the syncarps.

Of these species, *Artocarpus hirsutus*, from peninsular India, has an exceptionally long and slender male inflorescence indicating an affinity with sect. *Artocarpus*, but a subglobose to shortly cylindric syncarp covered by indurated, narrowly cylindric processes, which is somewhat similar to the syncarps of sect. *Duricarpus*. From the account given in Troup (Silvicult. Indian Trees 3: 876. *fig. 323*. 1921) it is evident that the mode of germination is also the same as that found in sect. *Duricarpus*. The characters of the perianth and ovary do not, however, appear to be in agreement. The internal structure of the mature syncarp is not known, but the submature fruiting perianths are thin and the ovary is membranous with a subapical style. In view of these differences, together with the shape of the male head and the complete absence of bracts from the inflorescences (although this last character may have arisen by parallel evolution), this species is assigned to sect. *Artocarpus*. The induration of the syncarp processes is assumed to be of less taxonomic importance, although it provides, together with the hispid twigs and the appearance of the leaves (the gland-hairs have a depressed-globose, c. 6-celled head), a superficial resemblance to *A. rigidus*.

The two other species, *Artocarpus nobilis* and *A. sepicanus*, are remarkable in that, although one comes from Ceylon and the other from New Guinea, they share the characters of narrowly cylindric inflorescences (cf. sect. *Artocarpus*) and well developed, peltate interfloral bracts (cf. sect. *Duricarpus*) which are persistent and conspicuous on the syncarps. In other respects, however, the appearance of the syncarps is very different: in *A. nobilis* the surface is covered by short, umbonate, indurated processes, while in *A. sepicanus* the syncarp is fleshy, with a pubescent, apparently completely smooth surface (cf. species of subg. *Pseudojaca*) and the styles are exserted through perforations in this. The internal structure is known only in *A. nobilis*, in which the fruiting perianths are thin, the ovary is pergamentaceous with a subapical style, and the symmetrical embryo lies obliquely in the median plane of the ovary with the relatively large radicle ventral (cf. series *Incisifolii*), although in its germination, as in *A. hirsutus*, the first pair of leaves is opposite. *A. nobilis* also shows an alliance with series *Incisifolii* in the shape of the gland-hairs, which have a peltate, flattened, 8-celled head, but in *A. sepicanus* the gland-hairs, which are

unusual in being deciduous at a very early stage, have a globose, 6–8-celled head.

These three species and, more especially, the curious resemblances between *A. nobilis* and *A. sepicanus* are a reminder of the long evolutionary history that can be assumed for this genus. It would appear that they are "relicts", and the persistence of a few such species that do not readily fit into a classification intended to reflect the affinities of the groups dominant today is scarcely surprising.

The series recognized within section *Artocarpus* are not, however, necessarily closely allied and it is not suggested that any one of them is directly ancestral to the others. Section *Duricarpus* may represent either an offshoot from sect. *Artocarpus* or an independent line of evolution within the genus. The anomalous species, as has already been implied, are probably the remnants of a wider variation exhibited by the genus in the past, and this may also be true of series *Cauliflori*.

KEY TO THE SPECIES OF ARTOCARPUS SUBGENUS ARTOCARPUS

1. Male head globose to clavate or short-cylindric, length/breadth = 1–3.5(–4), the surface largely covered by the peltate heads of numerous bracts; syncarp subglobose, length/breadth = 1–1.5, the surface covered by indurated processes; adult leaves pinnate or entire (rarely trilobed above the middle), the latter usually with fewer than 20 intercostals.[2]
   2. Syncarp processes narrowly cylindric, 5–8 × 1 mm., hispid, peduncle 4.5–6.5 cm. (male head narrowly cylindric, 7–16 × 0.5–0.7 cm.). Southern India. ..... 25. *A. hirsutus*.
   2. Syncarp not as above. Sect. Duricarpus.
      3. Twigs and leaves glabrous; male head ellipsoid to short-cylindric; syncarp processes glabrous or pubescent. Series Laevifolii.
         4. Leaves pinnate; syncarp processes elongate, narrowly cylindric, 6–8 × 1–1.5 mm., glabrous. Malaya, Sumatra, Borneo. ..... 1. *A. anisophyllus*.
         4. Leaves simple; syncarp processes short, broadly cylindric, truncate, c. 3.5 × 3 mm., and surface hence tesselate, or slightly tapering, obtuse, c. 1.5 × 1.5 mm., and somewhat separated, appressed-pubescent. Malaya, Sumatra, Borneo. ..... 2. *A. lanceifolius*.
      3. Twigs and leaves (at least on the main veins beneath) hispid or hispid-pubescent; male head globose to obovoid or clavate; syncarp processes hispid. Series Asperifolii.
         5. Syncarp processes broadly cylindric, 1.5–3.5 mm. long.
            6. Leaves smooth above, hispid-pubescent on the main veins only beneath; male peduncle 1–5 × 0.3 cm.; syncarp processes hispid from patent, usually slightly crisped hairs. Indochina, British North Borneo. ..... 3. *A. melinoxylus*.
            6. Leaves scabrid above, hispid-pubescent throughout beneath; male peduncle 6–7.5 × c. 0.15 cm.; syncarp processes hispid from appressed hairs. Northeastern India, Burma, Andaman and Nicobar Is. ..... 4. *A. chaplasha*.

[2] The intercostal veins should be counted along the distal side of a lateral vein near the middle of the leaf.

5. Syncarp processes elongate, 5–13 mm. long, narrowly cylindric with clavate tips, or tapering.
   7. Leaves hispid-pubescent above; male head 4–9 × 2.5–3.5 cm., peduncle 2.5–7 cm.; syncarp processes narrowly cylindric with clavate tips, 8–13 × 1 mm. Borneo, Philippines. ..... 5. *A. odoratissimus*.
   7. Leaves becoming smooth or scabrid above; male head to 3 × 2 cm., peduncle to 3 cm.; syncarp processes tapering, 5–9 × 1–1.5 mm.
      8. Twigs and peduncles patent-hispid; male peduncle 1.2–3 cm. Malaya. ..... 6. *A. hispidus*.
      8. Twigs and peduncles appressed-hispid; male peduncle 0.2–0.6 cm. Indochina, southern Burma and Siam, Malaya, Sumatra, Borneo, Java. ..... 7. *A. rigidus*.

1. Male head cylindric, varying ellipsoid or clavate, length/breadth = (1.5–)4–20, bracts usually very few or entirely lacking; syncarp ellipsoid to cylindric, varying to subglobose, length/breadth = 1–4, the surface covered by more or less fleshy, firm or flexuous processes (indurated in *A. nobilis* and *A. hirsutus*), varying to areolate or smooth; adult leaves pinnatifid to entire, the latter frequently with more than 20 intercostals. Sect. ARTOCARPUS.
   9. Inflorescences narrowly cylindric, the surface entirely or partly covered by the peltate heads of numerous bracts, persistent in both sexes.
      10. Twigs 10–12 mm. thick; leaves frequently distinctly and regularly crenate between the lateral veins; male head 7–13 × c. 1.5 cm.; syncarp to 20 × 10 cm., processes short-cylindric, obtuse, 1 × 1–1.5 cm., indurated. Ceylon. ..... 26. *A. nobilis*.
      10. Twigs 3–5 mm. thick; leaves not as above; male head to c. 3 × 0.5 cm.; syncarp to c. 4.5 × 1.5 cm., fleshy, surface (?) smooth, pubescent. New Guinea. ..... 27. *A. sepicanus*.
   9. Inflorescences not as above.
      11. Twigs appressed-hispid; male head narrowly cylindric, 7–16 × 0.5–0.7 cm.; syncarp to c. 5 × 4 cm., processes narrowly cylindric, 5–8 × 1 mm., rigid, hispid. Southern India. ..... 25. *A. hirsutus*.
      11. Male head not as above, *or* twigs subglabrous; syncarp not as above.
         12. Male head with the surface smooth; twigs glabrous, *or* villous from greyish, varying pale rufous hairs, *or* pilose or pungent from patent rufous hairs.
            13. Twigs (4–)6–22 mm. thick, villous, varying glabrous or with patent acicular hairs; adult leaves entire or pinnatifid; male head 1–30 × 0.7–3(–5.5) cm.; syncarp processes rough from the apices of deflexed, inflated hairs (except in *A. communis* and sometimes *A. horridus*), styles bifid or simple. Series INCISIFOLII.
               14. Adult leaves entire or pinnatifid, with up to 5(–9) pairs lateral lobes; inflorescences with all the flowers fertile; anthers 0.3–0.8 mm. long.
                  15. Adult leaves becoming entire; syncarp less than 10 cm. across, the processes (and the perianth lobes in the male head) rough from the apices of deflexed, inflated hairs *and/or* the twigs with rigid, patent, acicular hairs.

16. Twigs villous to glabrous; syncarp processes never glabrous.
    17. Male head 10–21 × 1.3–2 cm., anthers 0.7 mm. long; syncarp processes 8–15 × 1.5 mm.; inflorescences usually with scattered bracts. Mindoro, Luzon. ..... 8. *A. blancoi.*
    17. Male head 1–17 × c. 0.7 cm., anthers 0.3–0.5 mm. long; syncarp processes 2.5–4 × 2.5–3 mm.; inflorescences without bracts. Philippines. ... 9. *A. treculianus.*
16. Twigs with rigid, patent, acicular hairs, c. 2 mm. long; syncarp processes c. 3 × 1.5–3 mm., varying glabrous. Moluccas. ..... 10. *A. horridus.*

15. Adult leaves generally pinnatifid; syncarp more than 10 cm. across, the processes or facets (and the perianth lobes in the male head) with slender, patent hairs or glabrous (neither inflated nor acicular hairs present). ..... 11. *A. communis.*

14. Adult leaves deeply pinnatifid, with 7–20 pairs of lateral lobes; inflorescences often with solid, sterile, elongate flowers; anthers 1.2–1.5 mm. long.
    18. Lobes of leaf 12–20 pairs; male head with a few solid, cylindric perianths projecting to 0.5 mm. from the surface; syncarp processes all 3 × 2 mm., perforate, styles simple. Luzon. ..... 12. *A. pinnatisectus.*
    18. Lobes of leaf 7–10 pairs; male head with numerous solid, cylindric perianths with clavate tips projecting to c. 2 mm. from the surface; syncarp processes of two lengths, 15 × 1 mm., solid, and 5 × 1 mm., perforate, styles bifid. Samar, Mindanao.[3] ..... 13. *A. multifidus.*

13. Twigs 2–6 mm. thick, glabrous or pilose from patent, rufous hairs; adult leaves entire; male head 2–7.5 × 0.5–1.2 (–3) cm.; syncarp processes puberulent or minutely hispid, styles simple.
    19. Cauliflorous or ramiflorous; leaves with the lateral veins curved, 6–10 pairs; syncarp 15–100 × 10–50 cm., fruiting perianths markedly fleshy. Series Cauliflori.
        20. Twigs and peduncles usually pilose from patent, rufous hairs, c. 3 mm. long; base of leaf abrupt, intercostals to c. 10; inflorescences without a basal annulus. ..... 14. *A. integer.*
        20. Twigs and peduncles glabrous; base of leaf decurrent, intercostals c. 10–14; inflorescences with a

[3] The distribution of series *Incisifolii* within the Philippines is given as a rough guide only; the less common species will probably be found to occur more widely.

basal annulus formed by the enlargement of the top of the peduncle into a narrow flange. . . . . 15. *A. heterophyllus.*

19. Not cauliflorous or ramiflorous; leaves with the lateral veins straight; syncarps 6.5–8.5 × 2–3.5 cm., fruiting perianths not fleshy. Series ANGUSTICARPI.
    21. Leaves elliptic, lateral veins 11–16 pairs; male head without elongate solid perianths; syncarp with processes all perforate, conical and up to 1.5 mm. long, or the apices depressed and the surface hence areolate. Malaya, Sumatra. . . . . 16. *A. lowii.*
    21. Leaves ovate to ovate-elliptic, lateral veins 6–12 pairs; male head with filiform solid perianths projecting to 1 mm. from the surface; syncarp with processes mostly perforate, conical, to 1.5 mm. long, but a few solid, attenuate, to 4 mm. long. Nicobar Is., Malaya, Sumatra, Borneo, Celebes, Moluccas, New Guinea. . . . . 17. *A. teysmannii.*

12. Male head with the surface variously rugose; twigs hispid, hispid-pubescent or villous, the hairs usually rufous. Series RUGOSI.
    22. Shoots large to massive: twigs 5–20 mm. thick; male head 6–20 × 1–2.5 cm., the peduncle 3.5–10 cm.; syncarp 8–12 × 5–5.5 cm., usually with solid, flexuous processes, the peduncle 5.5–18 cm.
        23. Leaves with 11–16 pairs lateral veins; male head with the surface rugose-sulcate, not pilose; flexuous syncarp processes with short, patent, or long, appressed hairs.
            24. Twigs hispid, varying subglabrous; leaves thickly coriaceous; male head rugose-sulcate, perianths without crisped hairs; flexuous syncarp processes to 18 × 1.5 mm., shortly hispid, or none.
                25. Leaves smooth above, or nearly so; male head 6.5–10.5 × 1 cm.; syncarp with all processes c. 3 × 2 mm., or a few slightly elongate. Malaya, Sumatra. . . . . 18. *A. scortechinii.*
                25. Leaves scabrid above; male head 6–15 × 1.5–2.5 cm.; syncarp with flexuous processes 10–18 × 1–1.5 mm., shortly hispid. Peninsular Burma and Siam, Malaya, Sumatra, Borneo, Java, Lesser Sunda Is., Palawan. . . . . 19. *A. elasticus.*
            24. Twigs (often sparsely) villous; leaves coriaceous; male heads rugose or sub-tuberculate, perianths with crisped hairs; flexuous syncarp processes 20–35 × 0.5–1 mm., subappressed-pubescent, hairs to 2 mm. long. Borneo, Philippines, Celebes, Moluccas. . . . . 20. *A. sericicarpus.*
        23. Leaves with 15–23 pairs lateral veins; male head with the surface tuberculate from obtuse processes, c. 3 ×

2 mm., the apices pilose, hairs rufous, to 2 mm. long; flexuous syncarp processes to 10 × 0.5 mm., scabrid from recurved hairs. Borneo. ..... 21. *A. tamaran.*

22. Shoots smaller: twigs 2–3 mm. thick; male head 2–5.5 × 0.3–0.6 cm., the peduncle 0.5–2 cm.; syncarp 4–4.5 × 2–2.5 cm., without sterile processes, the peduncle 0.5–4 cm.

26. Leaves subappressed-pubescent throughout beneath; male peduncle c. 2 cm.; syncarp with acute conical processes. Sumatra. ..... 22. *A. sumatranus.*

26. Leaves usually appressed-pubescent on main veins only beneath; male peduncle to 1.3 cm.; syncarp with low, obtuse or truncate processes, or nearly smooth, the surface areolate.

27. Leaves elliptic-oblong varying elliptic, acute to acuminate, glabrous above; peduncles patent-pubescent, in male 0.7–1.3 cm., in female 1.5–4 cm.; syncarp pubescent, with low, obtuse processes, or nearly smooth, the surface areolate. Malaya, Sumatra, Borneo. ..... 23. *A. kemando.*

27. Leaves obovate-elliptic varying elliptic, shortly and obtusely acuminate to retuse, young leaves appressed-puberulent above; peduncles velutinous, in male c. 0.5 mm., in female 0.3–0.8 cm.; syncarp velutinous, tesselate from very low, truncate, processes. Malaya, Sumatra. ..... 24. *A. maingayi.*

Artificial keys for the identification of specimens bearing either male or female inflorescences are provided at the end of the treatment of this subgenus, and the second of these is illustrated.

Section **Duricarpus** Jarrett, sect. nov.

Folia adulta pinnata (*A. anisophyllus*) vel simplicia, integra, juvenilia pinnatifida; hypodermis absens, vel imperfectum, cellis elongatis compositum. *Inflorescentiae* bracteis interfloralibus peltatis, syncarpio subdeciduis. *Capitula mascula* subglobosa, obovoidea, clavata, ellipsoidea vel breviter cylindrica. *Syncarpia* globosa, vel subglobosa, processibus induratis obtecta; ovaria stylis terminalibus; semina testis pergamentaceis, rubris, pericarpiis induratis, perianthiis carnosisque inclusa; embryum in longitudinem positum, cotyledonibus aequalibus, radicula supera.

Type species: *Artocarpus rigidus* Blume.

Although the distinctive feature of this section is the syncarp, there is considerable variation in its appearance due to the differing shapes of the indurated processes (free perianth apices) covering it, which may be either narrowly cylindric (*A. anisophyllus* and *A. odoratissimus,* with clavate tips in the latter), or tapering so that the syncarp is echinate (*A. hispidus, A. rigidus*), or short and obtuse or truncate so that the surface is more or less clearly tessellated (*A. lanceifolius, A. melinoxylus, A. chaplasha*). Other characters, however, suggest that these resemblances do not neces-

sarily indicate the closest relationships of the species. *Artocarpus anisophyllus* stands out by reason of its pinnate leaves, but in the presence of a hypodermis, the deeply sunken gland-hairs, and the glabrous shoot, a close affinity is shown with *A. lanceifolius*, which is confirmed by the ellipsoid to cylindric male inflorescences, and the strongly differentiated endocarp. *Artocarpus odoratissimus*, *A. hispidus* and *A. rigidus* are likewise united by their obovoid, subglobose or clavate male inflorescences, the elongate, hispid syncarp processes, and the hispid shoots. Between them may be placed *A. melinoxylus* and *A. chaplasha*, which resemble the latter group in the characters of the shoot and the male inflorescence, but *A. lanceifolius* in the surface of the syncarp. These are the only two species in the section of which the distinctness is in any doubt, and the characters separating them are listed under *A. melinoxylus*. As noted above, two series are distinguished on the basis of leaf anatomy, indumentum of the shoot and shape of the male head, of which the first, series *Laevifolii*, includes *Artocarpus anisophyllus* and *A. lanceifolius*, while the rest of the species are placed in series *Asperifolii*.

Series **Laevifolii** Jarrett, ser. nov.

Ramuli et folia subglabri; folia hypoderme imperfecto, cellis elongatis composito, glandulis profunde immersis, capitibus globosis, 4–6-cellis; inflorescentiae masculae breviter ellipsoideae vel subcylindricae.

TYPE SPECIES: *Artocarpus anisophyllus* Miq.

1. **Artocarpus anisophyllus** Miq. Fl. Ind. Bat. Suppl. 422. 1861, "*anisophylla*;" Renner, Bot. Jahrb. **39**: 366. 1907; Merr. Pl. Elmer. Born. 45. 1929; Corner, Wayside Trees, 652. *t. 191, 192*. 1940. Holotype, Sumatra, *Teysmann HB 3698* (U); isotypes (BO, K, L).

Artocarpus klidang Boerl. Handl. Fl. Ned. Ind. **3**: 333, 371. 1900, in clavis.
Artocarpus superba Becc. For. Borneo, 625. 1902; Merr. Philip. Jour. Sci. **18**: 51. 1921, Enum. Philip. Pl. **2**: 43. 1923; Ridley, Fl. Malay Penin. **3**: 356. 1924. Holotype, Sarawak, *Beccari PB 2997* (FI); isotypes (FI, K).

Evergreen trees, height to 45 m. *Twigs* 10–20 mm. thick, rugose, appressed-puberulent and minutely punctate; annulate stipular scars c. 1.5 mm. broad, prominent; lenticels scattered. *Stipules* 4–17 cm. long, broadly ovate-lanceolate, acute, exterior rugose, subappressed-pubescent, hairs yellow to brown. *Leaves* imparipinnate; rachis 40–80 cm. (fide Elmer in Merrill, 1929, to 150 cm.) long, base to 7 mm. in diameter, terete, finely rugose; pinnae 5–12 on each side, usually in subopposite pairs with longer and shorter pairs alternating and the latter raised above the rachis, terminal pinna often bifid; juvenile leaves with distal pinnae decurrent on rachis and the pinnae pinnatifid; pinnae 3.5–40 × 2–13 cm., oblong to oblong- or ovate-lanceolate, with an acumen to 2 cm. long, the base rounded, varying cuneate, often inequilateral, glabrous, the margin entire or shallowly and distantly crenate; main veins prominent beneath, intercostals slightly so;

lateral veins 7–20 pairs, straight; intercostals parallel only towards margin; dark green, drying red-brown to pale greenish or yellowish brown; hypodermis of one cell-layer present, interrupted over the areolae, cells elongate in surface view; gland-hairs immersed, heads globose, 4–6-celled; petiolules to 40 mm. long.

Inflorescences, male and female heads usually paired in the same leaf-axil. *At anthesis*: *male head* 30–75 × 15–20 mm., ellipsoid-oblong, smooth, covered by flowers and bracts; perianths tubular, 1.8 mm. long, shortly bilobed above, minutely pubescent; stamen 2.0–2.3 mm. long, filament slender, cylindric, anther-cells subglobose, 0.2 mm. long; bracts slenderly stalked, heads infundibuliform, to 0.6 mm. across, pubescent; peduncle 50–65 × 4 mm., surface as in the twigs; *female head* with pubescent peltate bracts being shed and simple styles exserted to c. 1 mm. *Syncarp* to 11 × 8 cm. (fide Elmer, l.c., to 20 cm. in length), subglobose, brown, drying pale brown, covered by closely set, cylindric, rigid, shallowly fluted, obtuse, minutely punctate processes, 6–8 × 1–1.5 mm.; wall c. 6 mm. thick; fruiting perianths numerous, proximal free region orange, pulpy, "seeds" (endocarps) ellipsoid, 17 × 10 mm.; core c. 20 mm. across; peduncle 60–130 × 10 mm., surface as in the twigs.

VERNACULAR NAMES: *Bakil*, Sumatra, Borneo; *Mentawa* or *Mentaba*, Banka, Borneo; *Puan* or *Pupuan*, Borneo.

DISTRIBUTION: in evergreen forest to 4000 ft., Malaya, Sumatra, Banka, Billiton, Lingga, Borneo.

Malaya. MALACCA: *Maingay 1483* (K, ♂, ♀). SINGAPORE: Garden Jungle, *Ridley 4113* (CAL, SING, ♂), *6429* (BM, CAL, K, SING, ♀), *6678* (BM, CAL, K, SING, ♂, ♀); MacRitchie Reservoir, s. side, *Sinclair SFN 40658* (K, ♀); Seleter Reservoir, s. side, *Sinclair SFN 39249* (L, SING). (Fide Corner, 1940, frequent in lowland forest.)

Sumatra. INDRAGIRI: Kwala Belilas, *bb 27580* (A, BO, L); Muara Serangge, *bb 29991* (A, BO, L). BENKULEN: Lebong, Bosch Pengadang, *Olivier 29* (BO, L). PALEMBANG: Banjuasin, Bajunglintjir, *NIFS E 1028* (BO, ♀), *1163* (BO, L, U, ♀); Batu-radja, *Teysmann HB 3698* (BO, K, L, U); Lematang Ilir, Gunong Megang, *NIFS E 952* (BO, K, L, SING, U, ♀), *959* (BO, L, P, U, ♂, ♀), *1029* (BO, U, ♀); Lematang Ilir, Semangus, *bb 31984* (A, BO, SING), *32042* (BO, K); Lematang Ulu, *Grashoff 277* (BO); Muara Dua, *Grashoff 454* (BO, L); Rawas, *Grashoff 1052* (BO, L). LAMPONGS: Semangka, Kuta-Agung, *Gusdorf 289* (BO, L). BANKA: Lobok Besar, *Kostermans & Anta 1230* (A, L); Muntok, Batu-balai, *Teysmann 7245* (BO, C, K, L); Sungei Liat, *Teysmann 7247* (BO, C, K, L). BILLITON: *Rossum 48* (BO, L, ♂, ♀), *Teysmann s.n.*, (BO); Tandjungpandang, *Teysmann s.n.* (BO); Tandjungpandang, Bantan, *bb 8677*, (BO, L). LINGGA: *Teysmann 7282* (BO, L, P).

Borneo. SARAWAK. *Beccari PB 2997* (FI, K, ♀); Lundu, *Foxworthy 344* (L). WEST BORNEO. *De Vriese s.n.*, 1857–61 (BO [labelled *Riedel s.n.*, Menado, Celebes], L); Sanggau, Nek Sawah, *bb 14307* (BO). SOUTH AND SOUTHEAST BORNEO. Pleihari, Kintap, *bb 8145* (BO, L); Puruktjahu, Muara Djaan, *bb 10506* (BO, L); Tanah Bumbu, Kampong Baru, *bb 13053* (BO, L, ♂). EAST AND NORTHEAST BORNEO. Balikpapan: S. Tunan, *bb 25588* (BO, L). Berouw: Domaring, *bb 18861* (BO). Bulungan: Salim Botu, S. Kumoh, *bb 11275* (BO, L). E. Kutei: Bengalon

Rapak, *bb 15285*, *15319* (BO, L); Peridan, *bb 9862* (BO, L); Sangkulirang, Palawan, *bb 11859* (BO, L); Sangkulirang, Ronggang, *bb 7971* (BO, L); T. Leban, *bb 14685* (BO, L). W. Kutei: Blu-u, *Jaheri 1460* (BO); Ibo Antjalong, *bb 16484* (BO, P); Kahalâ, *bb 28365* (BO); Kelumpang, *bb 16928* (A, BO, L); Longbieh, *bb 16137* (A, BO, L), *16141* (BO), *16149* (BO, SING), *16152* (BO, P), *16488* (BO, SING); Mujup, *bb 16752* (A, BO, L). BRITISH NORTH BORNEO. Elphinstone Prov., Tawao, *Elmer 21600* (A, BM, BO, C, GH, K, L, P, SING, U, ♀); Kinabatangan Besar, Kori Timber Camp, *Cuadra A 2133* (K, SING); Mt. Kinabalu, Penibukan ridge, *Clemens 40424a*, *50210* (BM); Sepilok For. Res., 15 miles w. of Sandakan, *Wood SAN 16549* (A, K, L, ♂, ♀).

This species is the only one in *Artocarpus* to have pinnate adult leaves. It was noted by Corner (1940) that these are unusual both in that they do not disarticulate when falling, as do most compound leaves, and in the arrangement of the pinnae, with longer and shorter pairs alternating and the latter lying in a plane above the former (well shown in the photograph, l.c.). The only other occurrence of pinnate leaves in the genus appears to be in saplings of *A. tamaran*; the latter can readily be distinguished (apart from the indumentum of the shoot) by the continuous narrow wing of lamina on both sides of the rachis.

A sheet at Bogor identified under an unpublished name purports to have been collected by Riedel in Menado, Celebes, but this is presumably an error of labelling, since *De Vriese s.n.*, West Borneo, at Leiden, bears the same determination.

Merrill (1921, 1923) recorded this species (as *A. superba*) from Basilan (*Hutchinson FB 3989*), Mindanao (Zamboanga, *Merrill 8280*; Port Banga, *Whitford & Hutchinson FB 9164*; both sterile) and Palawan (*Cenabre et al. FB 28009*), but no duplicates of these collections have been traced.

2. **Artocarpus lanceifolius** Roxb. Fl. Ind. 3: 527. 1832, "*lanceaefolia*;" Wight, Ic. Ind. Or. 2: *t. 679*. 1843; Tréc. Ann. Sci. Nat. Bot. III. 8: 122. 1847; King in Hook. f. Fl. Brit. Ind. 5: 543. 1888; King, Ann. Bot. Gard. Calcutta 2: 13. *t. 11*. 1889; Renner, Bot. Jahrb. 39: 366. 1907; Ridley, Fl. Malay Penin. 3: 354. 1924; Foxworthy, Malayan For. Rec. 3: 128. *2 plates*. 1927; Burkill, Dict. 256. 1935; Corner, Wayside Trees, 656. *t. 197*. 1940.

Artocarpus lanceolfolia Roxb. Hort. Beng. 103. 1814, nomen nudum.

ssp. **lanceifolius**

Evergreen trees, height to 35 m., with small buttresses, bark dark grey, peeling off in flakes. *Twigs* 6–8 mm. thick, rugose, appressed-puberulent and minutely punctate; annulate stipular scars c. 1 mm. broad, inconspicuous; lenticels scattered. *Stipules* 1.5–4.5 cm. long, ovate-lanceolate, acute, exterior rugose, shortly appressed-pubescent. *Leaves* 10–33 × 5–17 cm., elliptic, varying to ovate, obovate or oblong, rarely narrowly lanceolate-elliptic, short-acuminate, acumen rounded varying acute, base cuneate, decurrent, rarely inequilateral, thickly coriaceous, glabrous, the margin entire or shallowly and distantly crenate; juvenile leaves pinnatifid; main

veins prominent beneath, reticulum not or scarcely prominent; lateral veins 9–14 pairs, straight; intercostals parallel; deep green, drying pale or reddish brown with straw-coloured reticulum; hypodermis of one cell-layer present, interrupted over the areolae, cells elongate in surface view; glands deeply sunken in narrow pits, heads globose, 4–6-celled; petiole 10–30 mm. long.

Inflorescences solitary in leaf-axils or the male ones paired. *At anthesis*: *male head* 30–60 × 12–18 mm., ellipsoid to cylindric, smooth, covered by flowers and bracts; perianths tubular, 2 mm. long, shortly bilobed above, puberulent; stamen 3.5 mm. long, filament slender, cylindric, anther-cells oblong, 0.4 mm. long; bracts slenderly stalked, heads infundibuliform, to 0.5 mm. across, sparsely ciliate; peduncle 25–70 × 2.5–5 mm., shortly appressed-pubescent; *female head* with pubescent peltate bracts mostly shed and bifid styles exserted to 0.5 mm. *Syncarp* to 8 × 7 cm. (to 12 cm. across, fide Foxworthy, 1927), subglobose, olive- or chestnut-brown, drying brown, tesselated from closely set, indurated, cylindric, truncate, appressed-pubescent processes, c. 3.5 × 3 mm.; wall c. 8 mm. thick; fruiting perianths numerous, proximal free region whitish, pulpy (fide Burkill, 1935), "seeds" (endocarps) ellipsoid, 20 × 10 mm.; core c. 15 mm. across; peduncle 50–100 × 8 mm., surface as in the twigs, or shortly appressed-pubescent.

Vernacular names: *Keledang* or *Klidang* (Malay), Malaya, Riouw-Lingga Archip. Uses: the timber is valuable and the pulp surrounding the seeds is eaten by jungle tribes.

Distribution: in evergreen forest to 2000 ft., Malaya, Sumatra (West and East Coast), Banka, Riouw-Lingga Archip.

Malaya. Perak. Larut: *King 3452* (BM, CAL, K, ♂), *3826* (CAL, K, ♀); Gunong Boobo Range, *King 7631* (CAL, K, P, SING, ♀). Pahang: Kuala Lipis, *Phillips 670* (SING); Temerloh, *Hamid CF 5737* (SING). Negri Sembilan: Gunong Angsi For. Res., *Sow 23728* (SING). Malacca: *Maingay 1478* (CAL, K, ♂, ♀); Bukit Sedanan Reserve, *CF 2100* (SING, ♂); Kesang tua, *Goodenough 1328* (BM, CAL, SING, ♀). Johore: Pulau Tinggi, above Kampong Tandjong Balang, *Sinclair s.n.*, May 1954 (SING); Pinerong, *Cantley 27* (K, ♂). Penang: Batu Ferengy, *Curtis 3654* (CAL, K, SING, ♀); Highlands, *Curtis 3602* (CAL, K, SING, ♂); Penang Hill, *Nanen 35845* (SING, ♀); Puram (?) Bukit, *Curtis s.n.*, July 1893 (SING). Singapore: Bukit Timah, *Corner s.n.*, Feb. 1931 (SING, ♀); Bukit Timah For. Res., Jalan Tiup Tiup, *Sinclair SFN 40249* (K, L); Gardens Jungle, *Ridley 6541* (BM, CAL, K, SING, ♂). (Fide Foxworthy, 1927, also in Kedah, Kelantan and Trengganu.)

Sumatra. West Coast: *de Vriese & Teysmann 20* (L); Padang, Lubuk peraku, *bb 6117* (BO); Painan, Barung Belantae, *NIFS SWK/I–50* (BO); near Pajakumbuh, Mt. Sago, *Meijer 4708* (CGE, ♀). East Coast: Simelungun, Masikat, *bb 5349* (BO, L); Sibolangit, *Lörzing 5445*, (BO, L, ♀). Banka: *Teysmann 7248* (BO, C, K, L, P); Muntok, Aer Limau, *bb 7613* (BO); Sungei-elan, *Teysmann 7250* (BO, C, K, L, P, ♀); Sungei-elan, Kampong permis, *Teysmann 7251* (BO, P, ♀). Riouw Archip.: Bintang, *Teysmann 7283* (BO, CAL, K, L, P, ♀). Lingga Archip. P. Sinkep: Bakong, *bb 2045*, *13670*, *Kassim 6* (BO, L); Bakong,

Santel, *bb 17400* (BO, SING); Djago, *bb 3945* (BO); Mapur, Marok Tuwa, *bb 3846* (BO); Tadjur Tandjong, *bb 8386* (BO); Tandjung Batang, *bb 4014* (BO, L).

Roxburgh's original description was very brief and no type specimen has been found, so that the identification must rest on his drawing of a leaf and a syncarp which was published by Wight in 1843 and can be recognized with certainty as representing this species.

ssp. **clementis** (Merrill) Jarrett, stat. nov.

Artocarpus clementis Merr. Jour. Str. Br. Asiat. Soc. **85**: 164. 1922. Holotype, British North Borneo, *Clemens 10770* (PNH, not seen, photograph in A); isotypes (A, BO, K).

Differs from ssp. *lanceifolius* as follows: *leaves* varying to ovate-elliptic or ovate-lanceolate; *syncarp* covered by somewhat widely spaced, indurated, slightly tapering, obtuse, appressed-pubescent processes, 1–1.5 × 1 mm., with scattered peltate bracts persistent between them; wall c. 3 mm. thick; "seeds" (endocarps) numerous, ellipsoid, 12–15 × 8 mm.; core c. 15 mm. across; peduncle 40 × 6 mm., minutely punctate.

VERNACULAR NAME: *Keledang* (Malay).

DISTRIBUTION: in evergreen forests to 3600 ft., endemic to northeastern Borneo.

Borneo. EAST AND NORTHEAST BORNEO. Balikpapan: Pemaluan, *bb 24763* (BO, L); S. Karnain, *bb 26374* (BO, L, SING). Berouw: Betemaran Tidi, *bb 19062* (BO); Domaring, *bb 18831* (A, BO), *bb 18835* (A, BO, L), *18851* (BO); Inaran, *bb 12078* (BO); Long Lanuk, *bb 18445* (BO), *18461* (BO, L, SING). Bulungan: Kabiran, S. Bengalun, *bb 11686* (BO); Mara, *bb 10750* (BO). E. Kutei: Muara Karangan, Remendai, *bb 7962* (BO); Sangkulirang, Palawan, *bb 11867* (BO); Sangkulirang, Pingadan, *bb 12992* (BO); Sangkulirang, Rantau Banan, *bb 15236, 15238, 15247* (BO); Loa Djanan, w. of Samarinda, *Kostermans 6627* (K, L, ♂); Tandjong Bangko, nr. Mahakam River estuary, *Kostermans 7096* (BO, K, L, ♀). W. Kutei: Djembajan, Sungei Djambu, *bb 24672* (A, BO, L); Kendisi, *bb 16681* (BO, L), *16695* (A, BO, L); Mo-Antjalong, *bb 16482, 16486* (A, BO, L); near Mt. Kemul, *Endert 3683* (L). Tidung: Loban, *bb 17882* (BO, L). BRITISH NORTH BORNEO. Mt. Kinabalu, *Foster & Puasa 3522* (K); Mt. Kinabalu, Gurulau Spur, *Clemens 10770*, Nov. 1915 (A, BO, K, ♀); 12 miles w. of Ranau, Bondu Tahan, *Wood & Charrington SAN 16381* (A, ♀). NUNUKAN. *bb 26174* (BO).

The description of the syncarp is based on that of the type of *Artocarpus clementis*, which is slightly decayed, but almost certainly had the processes rather widely spaced at maturity. In the other, younger, syncarps seen from Borneo the processes are also small but they are closely set and apparently separate only when the syncarp nears maturity. The three collections cited from British North Borneo have rather distinctive ovate-elliptic to ovate-lanceolate leaves, but they merely represent an extreme of the range of variation which is exhibited by the rest of the material seen from Borneo, nearly all sterile, and which is not separable from that of the species as a whole. In view of the discontinuity in the distribution of the species between a western area including Malaya and Sumatra and a smaller area

to the east in northeastern Borneo, it is likely that only ssp. *clementis* is represented in the latter. The sterile collections from Borneo are tentatively listed under this subspecies, but only specimens bearing syncarps or showing the extreme leaf-shape can be assigned here with certainty.

Series **Asperifolii** Jarrett, ser. nov.

Ramuli et folia hispidi vel hispidi-pubescentes; folia sine hypoderme, glandulis subimmersis, capitibus globosis, 4–16-cellis; inflorescentiae masculae globosae ad clavatae.

TYPE SPECIES: *Artocarpus rigidus* Blume.

3. **Artocarpus melinoxylus** Gagnep. Bull. Soc. Bot. Fr. **73**: 87. 1926, "*melinoxyla*;" Gagnep. in Lecomte, Fl. Gén. Indoch. **5**: 736. 1928. Syntypes, Indochina, *Chevalier 37007*, *Poilane 1218*, *4588*, *6873*, *7079*, *7621* (P); lectotype *Poilane 7079* (P).

ssp. **melinoxylus**

Trees, height to 15 m. *Twigs* 3–7 mm. thick, rugose, hispid, hairs yellow, appressed (longer and patent on juvenile shoots); annulate stipular scars 0.5 mm. broad, not or scarcely prominent; lenticels scattered. *Stipules* c. 2.5 cm. long, ovate, acute, hispid-pubescent, hairs yellow, subappressed. *Leaves* 7–30 × 4–18 cm. (–35 × 25 cm.) elliptic to obovate- or ovate-elliptic, short-acuminate, base rounded, varying cuneate, margin entire; main veins only prominent beneath or intercostals slightly so; glabrous above or with scattered hairs on the main veins, appressed subhispid-pubescent on the main veins beneath; lateral veins 6–13 pairs, straight, intercostals parallel; drying pale to dark red-brown, lighter beneath; hypodermis absent; glands half immersed, heads globose, 6–8-celled; petiole 8–28 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* (one only seen at maturity) 50 × 45 mm., subglobose, smooth, covered by flowers and bracts; perianths deeply 2(or 3)-lobed, 1 mm. long; stamen 1.5 mm. long, filament slender, cylindric, anther-cells ellipsoid, 0.2 mm. long; bracts stoutly stalked, heads peltate, to 0.4 mm. across, these and perianths sparsely ciliate; peduncle 50 × 3 mm., appressed hispid-pubescent; *female head* with pubescent peltate bracts mostly shed and simple styles exserted to 1.0 mm. *Syncarp* to 6 cm. across, globose, drying red-brown, covered by closely set, indurated, cylindric, obtuse, hispid processes, c. 3 × 2 mm., hairs patent and slightly crisped; wall c. 5 mm. thick; fruiting perianths numerous, proximal free region fleshy, "seeds" (pericarps) ellipsoid, 10 × 6 mm.; core 20–25 mm. across; peduncle 70–135 × 6 mm., appressed-hispid.

VERNACULAR NAME: *Cay mit nai*, Annam. USES: the wood is stated in field notes to be of good quality.

DISTRIBUTION: in forests to 5000 ft., endemic to Indochina.

Indochina. ANNAM. Near Huê, Nui Bah Ma, *Poilane 29977* (P, ♀). Near Nhatrang: Massif de Cô Ihn, *Poilane 4588*, Sept. 1922 (P, ♀); Massif de la Mère et l'Enfant, *Poilane 6873*, May 1923 (P, ♀). Quang Tri prov., Mai Lanh, *Poilane 1218*, Mar. 1920 (K, P, ♂). Near Tourane: *Clemens 3431* (P, ♂); Balete, *Clemens 4021* (K, P, ♀); Ba na, *Poilane 7079*, Aug. 1923 (A, P, ♀); Mt. Bani [Ba na], *Clemens 3510* (A, K, P, ♀); Lien Chien, *Poilane 7621*, Aug. 1923 (A, P, ♀); Thua-Luu div., Lang-co For. Res., *Chevalier 37007*, Apr. 1918 (P, ♂). LAOS. Luang Prabang prov., n.e. of M. Ngai [probably Muong Ngoi], *Poilane 20689* (P, ♂).

ssp. **brevipedunculatus** Jarrett, ssp. nov. Holotype, British North Borneo, *Wood SAN A 1733* (A); isotype (K).

Differt ab typo *inflorescentiis ad anthesin capitulis masculis* subglobosis, c. 15 mm. diametro, pedunculis, 8–17 × 2.5 mm. suffultis, *femineis* pedunculis 13–18 × 3 mm. suffultis [in syncarpio submaturo ad 25 mm. longis].

VERNACULAR NAME: *Temponek.*

DISTRIBUTION: in lowland forest, endemic to British North Borneo.

Borneo. BRITISH NORTH BORNEO: Beaufort, *Wood SAN A 1733*, May 1955 (A, K, ♂, ♀); Jesselton, *Daw Kepong FN 71664* (A, K, ♀).

This new subspecies agrees closely with the type from Indochina, except in the smaller size of the male head and in the length of the peduncles. The elongation of the latter, throughout the genus, occurs largely before anthesis and they can be assumed to be considerably shorter than in ssp. *melinoxylus*, even in the mature syncarp. In spite of the difference in the size of the male inflorescence in the two subspecies the dimensions of the flowers are the same; the perianths are unusual for this subgenus in that they are very deeply lobed.

Although taxonomically *Artocarpus melinoxylus* is very near *A. chaplasha*, it differs in a number of characters which appear to justify maintaining it as a distinct species. The male inflorescence in *A. chaplasha* has a longer, more slender peduncle and the flowers are larger in all their parts, while the perianth is only shortly bilobed. The indumentum of the syncarps is also different, being appressed on the syncarp processes in *A. chaplasha* instead of patent and slightly crisped. In *A. chaplasha* the leaves have the entire upper surface and the venation beneath subappressed hispid-pubescent, but in *A. melinoxylus* the leaves have a smooth upper surface and only the main veins are appressed hispid-pubescent beneath.

4. **Artocarpus chaplasha** Roxb. Hort. Beng. 66. 1814, nomen nudum, Fl. Ind. 3: 525. 1832; Wight, Ic. Ind. Or. 2: *t. 682*. 1843; Tréc. Ann. Sci. Nat. Bot. III. 8: 112. 1847; Kurz, For. Fl. Burma 2: 432. 1877; King in Hook. f. Fl. Brit. Ind. 5: 543. 1888; King, Ann. Bot. Gard. Calcutta 2: 13. *t. 12*. 1889; Renner, Bot. Jahrb. 39: 365. 1907; Troup, Silvicult. Ind. Trees 3: 880. *t. 325*. 1921; Parkinson, For. Fl. Andaman Is. 254. 1923; Champion, Indian For. 60: 524. *t. 50*. 1934. Holotype, "East India," *Roxburgh s.n.* (K).

Artocarpus chama Buch.-Ham. ex Wall. Cat. no. 4657C. 1831, nomen nudum.
Urostigma chrysophthalmum Miq. Hook. Lond. Jour. Bot. 6: 575. 1847.
Ficus chrysophthalma Miq. Ann. Mus. Lugd.-Bat. 3: 285. 1867.

Deciduous trees, height to 40 m., bark grey, becoming brown, peeling off in flakes. *Twigs* 4–10 mm. thick, rugose, densely hispid-pubescent, hairs yellow, appressed (patent on juvenile shoots); annulate stipular scars c. 0.5 mm. broad, not or scarcely prominent; lenticels scattered. *Stipules* 1.5–2.5 cm. long, ovate-lanceolate, acute, hispid-pubescent, hairs yellow, appressed. *Leaves* 14–23 × 9–14 cm., obovate-oblong, varying obovate or elliptic, acute, base rounded or shallowly cordate, margin entire; juvenile leaves pinnatifid; main veins prominent beneath, intercostals slightly so; very shortly subappressed-hispid above, venation beneath shortly subappressed hispid-pubescent, both surfaces varying subglabrous; lateral veins 8–12 pairs, straight; intercostals parallel; green, drying pale or reddish brown, lighter beneath; hypodermis absent; glands half immersed, heads depressed-globose, c. 8-celled; petiole 8–30 (–40) mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 15–30 × 10–30 mm., ellipsoid to short-obovoid or subglobose, smooth, covered by flowers and bracts; perianths tubular, 2 mm. long, bilobed above, minutely pubescent; stamen 2.5 mm. long, filament slender, cylindric, anther-cells ellipsoid, 0.3 mm. long; bracts slenderly stalked, the heads peltate, to 0.5 mm. across, pubescent; peduncle 60–75 × 1.5 mm., shortly appressed hispid-pubescent; *female head* with pubescent peltate bracts mostly shed and simple styles exserted to 0.5 mm. *Syncarp* to 6 cm. [to 10 cm., fide King, 1889] across, subglobose, yellow, drying brown, covered by closely set, indurated, cylindric, obtuse, appressed-hispid processes, c. 1.5 × 2 mm.; wall c. 5 mm. thick; fruiting perianths numerous, proximal free region . . . , "seeds" (pericarps) ellipsoid, 7 × 4 mm. [fide King, 1889, to 20 mm. long]; core c. 20 mm. across; peduncle 55–80 × 3 mm., appressed hispid-pubescent.

Vernacular names: *Chaplash* (Bengali), India; [4] *Taung-peing*, Burma. Uses: an important timber tree and often planted, although Champion (1934) stated that elephants found the seedlings very palatable; Parkinson (1923) noted that the leaves were used for elephant fodder and the fruits were edible.

Distribution: in evergreen, semi-evergreen and moist deciduous forest to 5000 ft., in regions with a monsoon climate (rainfall at least 80 inches), northeastern India (Sikkim to Assam and Chittagong), Lower Burma (to northern Tenasserim), Andaman and Nicobar Is.

India. Not localized: East India, *Roxburgh s.n.* (K); Dulka Thae, *Gamble 1180A*, Jan. 1873 (K); Majoojah forests, *Brandis 331*, Jan. 1862 (BM). Sikkim: *Anderson s.n.* (BO), *Hooker f. & Thomson s.n.* (CAL, GH, P), *Kurz s.n.* (CAL); Terai, Tin sing tung, *sine nom. et num.* (K). West and East Bengal: Duars,

[4] Throughout this series of papers the word India will be used in a geographical sense, to denote the Indian subcontinent, and will include the modern political subdivisions of India and Pakistan.

Talpaigwa, *Haines 529* (K); towards Ilafoo, *Griffith 4668* (K); Tipperah (Hill), near Ranir Bazar, Noagaon, *Debbarman 1096* (CAL, ♀). ASSAM: *Lister s.n.* (CAL), *Mann s.n.* (CAL, ♂), *Masters s.n.* (BO, L, P); Abor, Pilung, *Burkill 38127* (CAL); Gowhatly, *Clarke 37165A* (BM); [? =] Guwalatty, near Aber [? Abor], *Jenkins s.n.*, Apr. 1835 (CAL); Cachar, Bundookmora, *Keenan s.n.* (K); Jatookia, *Watt 11308* (BM, ♂); Kamrup, *sine nom. 942* (CAL, ♂); Khasia Hills, *Hooker f. & Thomson s.n.* (A, BM, C, L, P, U); Khasia Hills, Doodputli, *Hooker f. & Thomson s.n.*, Nov. 1856 (K); Mangeldai to foot of Bhutan Himalaya, *Schlagintweit 13480* (BM); Naga Hills, *Mohassi 214* (L); Nowgong, *Hooker f. & Thomson s.n.*, July 1850 (K); Sibsagar, Ligri Pukri, *Watt 10405* (CAL, ♀). CHITTAGONG: Kagi Ke Hath, *Hooker f. & Thomson s.n.*, Jan. 1851 (K); Kodala. *Hooper 26008* (CAL), *King 392, 487* (BM, CAL, ♀); Rangamati, *Lister s.n.* (CAL); Rangamati, Magban, *Hooper s.n.*, Nov. 1898 (CAL); Rangamati and Damara, *Wallich 4657C* (BM); Seetakoone, *Hooker f. & Thomson s.n.*, Jan. 1851 (K).

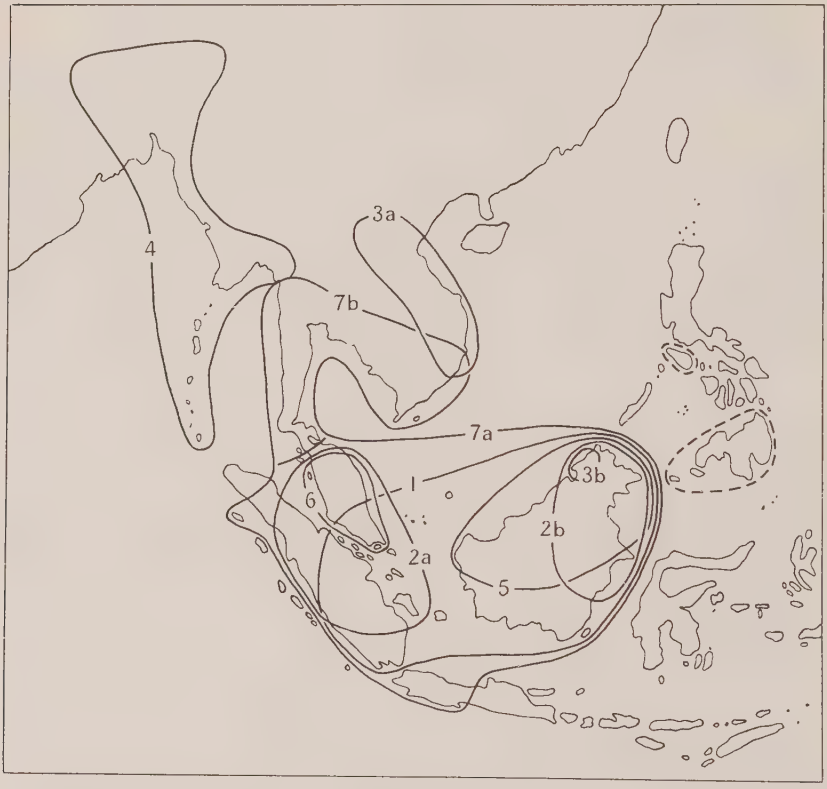


FIG. 11. Distribution of the species of sect. DURICARPUS. 1, *Artocarpus anisophyllus* (? also in the Philippines); 2, *A. lanceifolius*, a, ssp. *lanceifolius*, b, ssp. *clementis*; 3, *A. melinoxylus*, a, ssp. *melinoxylus*, b, ssp. *brevipedunculatus*; 4, *A. chaplasha*; 5, *A. odoratissimus* (probably introduced in the areas enclosed by broken lines); 6, *A. hispidus*; 7, *A. rigidus*, a, ssp. *rigidus*, b, ssp. *asperulus*.

Lower Burma. (?) *Abel s.n.* ["East Indies"] (*K*, ♂); Pegu, Tonkyeghat, *Kurz 1498* (CAL p.p., L, ♀), *1499* (CAL); Rangoon, *Dickason 5528*, *6948* (A), *McClelland s.n.* (K, ♂). TENASSERIM. Kyauktalon [not located], *Meebold 14612* (CAL, ♂). Thaton: Martaban, *Kurz 1498* (CAL p.p., ♀). **Andaman Islands.** *Kurz s.n.*, Nov. 1881 (CAL), *Parkinson 167* (DD, ♂), *Rogers s.n.*, 1904 (K, ♂, ♀); Manglutan, *Parkinson 463* (K, ♂ ♀); South Andaman, *King s.n.*, Apr. 1890 (CAL), *Kurz s.n.* (K, ♀); South Andaman, n. coast, *Kurz s.n.* (K, ♀); S. Andaman, S. Corbyn's Cove, *Kurz s.n.* (CAL). **Nicobar Islands.** *Jelinek 165* (CAL, ♂); Karnicobar, Kakena, *Kamphovener 2672* (C); Karnicobar and Chowry, *Kamphovener 2394* (C); Teressa, *Kamphovener 2741*, *2742* (C).

Cultivated. INDIA: Calcutta, Hort. Bot., *Lane 7935* (CAL, ♂), *Wallich 4657* (K, ♂), *4657D* (BM, CGE, P, ♂), *s.n.*, Apr. 1815 (C); Dehra Dun, Forest Research Institute, *Raizada s.n.*, May 1947 (DD, ♂, ♀), *s.n.*, June 1950 (DD, ♀).

Artocarpus chaplasha is somewhat similar vegetatively to *A. rigidus* ssp. *asperulus* (in addition to *A. melinoxylus*, the distinguishing characters of which have been given above), but it may be identified by the larger, typically obovate-oblong leaf, since in Tenasserim where the two entities may overlap, the leaf shape of *A. rigidus* ssp. *asperulus* tends to ovate. It is, however, of interest to note that the distributional areas of these three entities, and hence, presumably, their ecological requirements are complementary. *A. chaplasha* is restricted to areas with a moderate to well-marked monsoon climate (but a rainfall of at least 80 inches) and is recorded definitely as far south as the Thaton district of Tenasserim. *A. rigidus* ssp. *asperulus* is recorded only as far north as the adjacent Amherst district (there is one unlocalized collection by Meebold of each species) and occurs, primarily in coastal areas, in the moister peninsular regions of Burma and Siam, extending to Cambodia and southern Annam; it is replaced by *A. melinoxylus* in the mountains of Annam and northeastern Laos, which have a rather more uniform, though not more abundant, rainfall.

5. **Artocarpus odoratissimus** Blanco, Fl. Filip. 671. 1837, "*Arctocarpus odoratissima*;" Fern.-Villar, Noviss. App. 203. 1880; Elmer, Leafl. Philip. Bot. **2**: 618. 1909; Wester, Philip. Agr. Rev. **8**: 108. *t. 7d*, *9b*. 1915. **17**: 24. 1924(a), Bull. Bur. Agr. Philip. **39**: 129, *t. 15b*, *32b*. 1924(b); Merr. Jour. Str. Br. Asiat. Soc. **76**: 80. 1917, Sp. Blancoanae. 124. 1918, Enum. Philip. Pl. **2**: 42. 1923. Neotype, Mindoro, *Merrill SB 1019* (BM).

Artocarpus tarap Becc. For. Borneo, 626. 1902; Renner, Bot. Jahrb. **39**: 365. 1907. Syntypes, Sarawak, *Beccari PB 9*, *PB 2528*, *PB 2588*, *PB 2697* (FI); lectotype, *Beccari PB 2697* (FI).

Artocarpus mutabilis Becc. For. Borneo, 627. 1902; Renner, Bot. Jahrb. **29**: 365. 1907. Holotype, Sarawak, *Beccari PB 758* (FI); isotypes (FI, K, P).

Evergreen trees, height to 25 m. *Twigs* 4–10 mm. thick, rugose, hispid-pubescent, hairs yellow to rufous, patent; annulate stipular scars c. 0.5 mm. wide, not raised; lenticels scattered. *Stipules* 1–8 cm. long, ovate, acute, hispid-pubescent, hairs yellow to rufous, appressed or patent. *Leaves* 16–50 × 11–28 cm., broadly elliptic to obovate, obtuse to shortly acumi-

nate, base cuneate, often slightly decurrent, margin entire or distantly and shallowly crenate, often bearing tufts of hairs towards and at apex, varying lobed in upper half, lobes one (rarely two) on each side; juvenile leaves pinnatifid; main veins and intercostals prominent beneath, reticulum slightly so; both surfaces subappressed hispid-pubescent, scabrescent above, with the main veins softly and densely yellowish pubescent; lateral veins 13–15 pairs, straight; intercostals parallel; dark green, drying reddish to blueish brown above, red-brown beneath; hypodermis absent; glands slightly sunken, heads globose (8–)16-celled, cells in two tiers; petiole, 20–30 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 40–90 × 25–35 mm., ellipsoid to clavate, smooth, covered by flowers and bracts; perianths tubular, 1.8 mm. long, shortly bilobed above, minutely pubescent; stamen 2.0 mm. long, filament slender, cylindric, anther-cells subglobose, 0.15 mm. long; bracts slenderly stalked, heads peltate, to 0.4 mm. across, pubescent; peduncle 25–70 × 3–5 mm., indumentum as shoot; *female head* with pubescent peltate bracts mostly shed and simple styles exserted to c. 1.5 mm. *Syncarp* to 16 × 13 cm., subglobose, greenish yellow, drying pale red-brown, covered by closely set, rigid, cylindric, hispid processes, 8–13 × 1 mm., fluted below, the tips clavate; wall c. 8 mm. thick; fruiting perianths numerous, proximal free region white, juicy (fide Wester, 1915), "seeds" (pericarps) ellipsoid, 12 × 8 mm.; core c. 15 mm. across; peduncle 55–140 × 8 mm., indumentum as shoot.

VERNACULAR NAMES: *Oloi* or *Loloi*, Mindoro; *Marang* or *Madang*, Mindanao, Basilan, Sulu; *Tcrap* (Malay), Borneo. USES: the syncarp is esteemed, particularly in the Philippines, for the sweet, juicy, aromatic perianths surrounding the seeds, which may also be roasted; according to Wester (1915) the flavour is better than that of the Jack.

DISTRIBUTION: in evergreen forest to 3000 ft., Borneo; in regions with abundant and equally distributed rainfall (? introduced), Philippines (Mindoro, Mindanao, Basilan, Sulu Archip.).

Borneo. *Korthals s.n.* (L, U). SARAWAK. *Haviland 3116C* (CAL, ♂, ♀); Upper Rejang River, Gat, *Clemens s.n.*, July 1922 (NY); Gunong Mattan, *Beccari PB 2528*, Nov. 1866 (FI, K), *2588*, Nov. 1866 (FI, K, P, ♂, ♀); Kuching, *Beccari PB 2697*, Nov. 1866 (FI, K, ♀), *Haviland 2190* (CAL, K, SING, ♂, ♀), *Haviland & Hose 3316* (K, ♂, ♀), *3316B* (BM, L, ♂, ♀); base of Santubong, *Sinclair SFN 38372* (K, SING, ♀); Siul, nr. Kuching, *Beccari PB 758*, Oct. 1865 (FI, K, P, ♂, ♀). WEST BORNEO. *De Vriese s.n.* (K); Landak, *s. nom. et num.* (BO); Liang gagang, *Hallier 2577* (BO); Melawie, Tjatil B. Tengkujung, *bb 26328* (BO, L). SOUTH AND SOUTHEAST BORNEO. Muara Teweh, Lué Katjang, *bb 10926* (BO); Puruktjahu, Muara Djaan, *bb 10514* (BO). EAST AND NORTHEAST BORNEO. Berouw: Dedemuaer, *bb 19103* (A, BO, L); Tandjong-redeb, Labanan, *bb 11520* (BO). Tidung: *bb 17732* (BO); G. Muara Tagel, *Amdjah 136* (BO, L, ♀). W. Kutei: Blu-u, *Jaheri 1488* (BO). BRITISH NORTH BORNEO. *Burbridge s.n.*, 1877–78 (BM, K); Kabili-Sepilok For. Res., *Puasa Herb. For. Dept. B.N.B. 7037* (SING); Mt. Kinabalu, Dallas, *Clemens 26228* (A, BM, BO, L, NY, SING, ♀); Tenom, Pangie mile 80, *Cuadra A 3282* (L, SING). SIBATIK. St. Lucia, *Cuadra*

A 2403 (K, L). NUNUKAN. *bb 26196* (BO, L). TARAKAN. N. E. Kalimantan, Passanggrahan, *Meijer 1851* (K, L, ♀).

Philippine Islands. MINDORO. Calapan, *Merrill 2583* (US, ♂), *SB 1019*, May 1916 (A, BM, BO, GH, K, L, P, ♀); Pinamalayan, *Ramos BS 41090* (A, ♀); Upper Sinariri River ("near house"), *Conklin PNH 17522* (A, L, PNH, ♀). MINDANAO. Davao: *Wester BS 19356* (K, ♀). Lanao: near Abaga ("probably planted"), *Lynn Zwickey 243* (A, ♂). Zamboanga: *Ramos & Edano BS 37469* (A, BM, L, ♀). BASILAN. *Hallier 4504* (L), *Merrill SB 1018* (A, BM, BO, GH, K, L, P), *Miranda FB 17880* (K, P, ♂), *Reillo FB 15416* (L), *Wester BS 38345* (A); San Rafael, Moro, *Hutchinson s.n.*, May 1906 (NY). SULU ARCHIP. Jolo, *Vidal 3846* (K). **Cultivated.** BORNEO. Sarawak, *Beccari PB 9*, May 1865 (FI, K, P, ♂); Sandakan, *Villamil Herb. For. Dept. B.N.B. 200* (L). MAURITIUS. *Chapelier s.n.*, *Commerson s.n.* (P).

Apart from the very characteristic inflorescences, this species can be recognized by the length of the indumentum on both surfaces of the leaves. In *Artocarpus elasticus*, which may be confused with *A. odoratissimus* when sterile, the leaves are also markedly scabrid above, but from very short appressed hairs.

Although this species was described from and is better known in the Philippines, its distribution there is limited and it was probably introduced to the islands from Borneo, where it was described under the names *A. mutabilis* and *A. tarap* by Beccari. The second of these was reduced to *A. odoratissimus* by Merrill (1917) and later he stated (1924) that the species apparently was always planted in the Philippines, which is confirmed by such field notes as are available (quoted above). Wester (1924a) also noted a tradition of the Moros in the southwestern Philippines that the Marang was introduced by them from the west.

6. **Artocarpus hispidus** Jarrett, sp. nov. Holotype, Singapore, *Corner SFN 37035* (SING); isotype (K).

Differt ab *A. rigido* capitulis masculis longiore pedunculatis, ramulis juvenilibus pedunculisque dense hispidi-pubescentibus, pilis patentibus.

Arbores [ad 20 m. altae]. *Ramuli juniores* 4–7 mm. crassi, plus minusve rugosi, dense hispidi-pubescentes, pilis rufis patentibus; cicatrices stipularum annulatae, 0.5 mm. latae, non prominentes, nec conspicuae; lenticellae rarae. *Stipulae* 0.5–1[–2] cm. longae, ovatae, acutae, dense subappresseque hispidae, pilis rufis. *Folia* 15–19 × 7–8 [12–23 × 5–10] cm., obovati-elliptica [vel elliptica], acuta [vel breviter acuminata] basi cuneata, margine versus apicem denticulata [vel integra], supra scabrida, pilis brevissimis appressis praefractisve, basibus inflatis tuberculatis, costa nervis lateralibusque dense appresseque pubescentibus, subtus hispidi-pubescentia, saturata virida, in sicco rubri-brunnea, vel supra canescentia; folia juvenilia pinnatifida; costa nervi lateralesque subtus prominentes; nervi transversales venulaeque subtus prominuli; nervi laterales utrinque [11–]14–15, recti; nervi transversales paralleli; hypodermis absens; glandulae subimmersae, capitibus globosis, 4–8-cellis; petiolus 10–15[–20] mm. longus.

Inflorescentiae axillis foliorum solitariae [vel geminae]. *Ad anthesin*: *capitula mascula* [15–]30 × [15–]20 mm., obovoidea, plana, floribus bracteisque numerosissimis obtecta; perianthia tubulosa, 0.6 mm. longa, supra bilobata, minute pubescentia; stamina 0.7 mm. longa, filamentis tenuis, cylindricis, cellis antherum globosis, 0.1 mm. longis; bracteae tenuiter stipitatae, capitibus peltatis, ad 0.3 mm. latis, pubescentibus; pedunculus 25[12–30] × 2 mm., indumento ut ramulis; *capitula feminea* bracteis peltatis pubescentibus subdeciduis, stylis simplicibus 1.5 mm. longis exsertis. *Syncarpia* ad 5.5 cm. diametro, globosa, in sicco fulvi-brunnea, echinata, processibus crebris, rigidis, teretibus, obtusis, hispidis, 5–6 × 1 mm.; stratum externum syncarpii c. 2 mm. crassum; "semina" (pericarpia indurata) numerosa, ellipsoidea, 13 × 10 mm., perianthiis liberis carnosisque inclusa; axis syncarpii c. 15 mm. diametro; pedunculus 25–35 × 5 mm., indumento ut ramulis. (Inflorescentiae typi spiritu vini conservae descriptae.)

DISTRIBUTION: in evergreen forest to 1000 ft., endemic to Malaya.

Malaya. PERAK: Goping, *Scortechini 1979* (BM, CAL, K, SING, ♂, ♀). TRENGGANU: Kg. Binjai, on road to K. Brang, *Corner s.n.*, Apr. 1937 (SING). SELANGOR: Sungei Buloh For. Res., *Ja'amat & Jackson SFN 39416* (A, L, ♂). MALACCA: *Cantley s.n.* (SING, ♂). PENANG: Government Hill, *Curtis s.n.*, Mar. 1894 (SING). SINGAPORE: Bukit Timah, *Corner SFN 37035*, June 1940 (K, SING, ♂, ♀). *Corner s.n.*, Mar. 1941 (SING, ♂); Changi, *Ridley 3357* (BM, CAL, SING, ♀); 11½ miles Mandai road, *Sinclair SFN 40051* (L); Reservoir jungle, Thompson Reach end, *Corner s.n.*, Jan. 1937 (SING); Sangli, *Ridley 6756* (SING, ♂). **Cultivated.** SINGAPORE: Hort. Bot., *Ahmad s.n.*, Mar. 1926 (SING, ♂).

The syncarps of *Artocarpus hispidus* and *A. rigidus* are very similar but the two species are quite distinct in the length of the male peduncles and the indumentum of the shoot and peduncles, and the differences were noted by Corner on the type. *Artocarpus hispidus* also differs from *A. rigidus* ssp. *rigidus* in the scabrid upper surface of the leaf, and from ssp. *asperulus* in the leaf shape. King's description of *A. rigidus*, under which he cited *Scortechini 1979*, also included this species.

7. **Artocarpus rigidus** Blume, Bijdr. 482. 1825, "*rigida*;" Tréc. Ann. Sci. Nat. Bot. III. 8: 114. 1847; Miq. in Zoll. Syst. Verz. Ind. Archip. 2: 89, 95. 1854; Miq. Fl. Ind. Bat. 1(2): 286. 1859, Suppl. 418. 1861, Ann. Mus. Lugd.-Bat. 3: 211. 1867, Kurz, For. Fl. Burma 2: 431. 1877; King in Hook. f. Fl. Brit. Ind. 5: 540. 1888; King, Ann. Bot. Gard. Calcutta 2: 8. *t. 3*. 1889; Koord. & Val. Bijdr. Boomsoort. Java 11: 17. 1906; Renner, Bot. Jahrb. 39: 366. 1907; Ridley, Fl. Malay Penin. 3: 352. 1924; Corner, Wayside Trees, 657. *t. 198, 199*. 1940; Backer, Beknopte Fl. Java 6: 14. 1948. Holotype, Java, *Blume 1364* (L); isotype (CAL).

Artocarpus runcinata Reinw. ex Blume, Cat. Bog. 101. 1823, nomen nudum. *Artocarpus echinata* Roxb. Hort. Beng. 66. 1814, nomen nudum. Fl. Ind. 3:

527. 1832; Wight, Ic. Ind. Or. 2: *t. 680.* 1843; Tréc. Ann. Sci. Nat. Bot. III. 8: 113. 1847. Holotype, *Roxburgh s.n.* (BM).

Artocarpus cuspidatus Griffith, Not. Pl. Asiat. 4: 400. 1854. Holotype, Malacca, *Griffith 4664* (K).

Artocarpus kertau Zoll. ex Miq. in Zoll. Syst. Verz. Ind. Archip. 2: 89, 95. 1854; Miq. Fl. Ind. Bat. 1(2): 287. 1859; Koord. Exkursionsfl. Java 2: 95. 1912. Holotype, Java, *Zollinger 1009* (P); isotypes (L, U).

Artocarpus dimorphophylla Miq. Fl. Ind. Bat. Suppl. 417. 1861, Ann. Mus. Lugd.-Bat. 3: 211. 1867. Holotype, Sumatra, *Teysmann HB 3369* (U); isotype (BO).

Artocarpus varians Miq. ll.cc. Holotype, Sumatra, *Teysmann HB 4358* (U); isotypes (BO, L).

Artocarpus muricata Hunter ex Ridley, Jour. Str. Br. Asiat. Soc. 53: 114. 1909, pro syn.

ssp. **rigidus**

Evergreen trees, height to 35 m., buttressed, bark grey, peeling off in flakes. *Twigs* 2–6 mm. thick, smooth or rugose, densely to sparsely hispid, hairs rufous, appressed; annulate stipular scars c. 0.5 mm. broad, inconspicuous; lenticels few, scattered, or none. *Stipules* 0.5–3 cm. long, ovate-lanceolate, acute, hispid-pubescent, hairs yellow or rufous, appressed. *Leaves* 9–32 × 5–15 cm., elliptic to ovate-, obovate- or oblong-elliptic, apex acute or short-acuminate, varying obtuse, base cuneate, varying narrowly rounded, margin entire or distantly and shallowly crenate; juvenile leaves pinnatifid; main veins and intercostals prominent beneath, reticulum slightly so; glabrous and smooth above, or rarely slightly scabrid from sparse, very short, appressed hairs, except the appressed-pubescent main veins, venation appressed-hispid beneath; lateral veins (9–)12–20 pairs, straight; intercostals parallel; dark green, drying blue-grey to red-brown above, red-brown beneath; hypodermis absent; glands slightly sunken, heads globose, 8-celled, cells in two tiers; petiole 10–25 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 13–20 mm. across, short-obovoid to globose, smooth, covered by flowers and bracts; perianths tubular, 1.2 mm. long, shortly bilobed above, minutely pubescent; stamen 1.3 mm. long, filament slender, cylindric, anther-cells globose, 0.1 mm. long; bracts slenderly stalked, heads peltate, to 0.3 mm. across, shortly ciliate; peduncle 2–6 × 2.5 mm., densely appressed hispid; *female head* with pubescent peltate bracts being shed, and simple styles exserted to c. 5 mm. *Syncarp* to 7 cm. across (to 13 cm. fide Corner, 1940) globose, dull orange, drying pale brown, echinate from closely set, rigid, tapering, fluted, acute, hispidulous processes, 7–9 × 1.5 mm.; wall c. 10 mm. thick; fruiting perianths numerous, proximal free region orange, fleshy, "seeds" (pericarps) ellipsoid, 12 × 7 mm.; core c. 20 mm. across; peduncle 8–25(–40) × 8 mm., appressed hispid.

VERNACULAR NAMES: *Perian,* Malaya, *Purian* or *Surian,* Sumatra, *Pujan,* Borneo (Malay); *Tempunai* or *Tempunih,* Malaya, *Tempunit,* Sumatra (Malay); *Pussar,* Java (Sundanese). USES: the tree is cultivated for its

fruit in Malaya and Java, the edible portion being the sweet, pulpy, waxy perianths surrounding the seeds; it also provides timber.

DISTRIBUTION: in evergreen forest to 1500(–3000) ft., noted several times as occurring near streams, Tenasserim, Malaya, Sumatra, Simalur, Banka, Billiton, Riouw-Lingga Archip., Borneo, Java (except the eastern province).

Lower Burma. TENASSERIM: *Helfer 4669* (CAL, K, ♂). **Malaya.** KEDAH: Bukit Rombang, *Dmat Kepong FN 27377* (K, ♂); Cherok Perah, *Meh CF 17779* (SING); Katumbah, *Meh CF 17882* (SING). PERAK: *King 6921* (CAL, K, ♂, ♀); Batang Padang district, *King 7755* (CAL, K, L, P, ♀); Bikum Sungei, *Murdoch 376* (BM); Larut, *King 6727* (CAL, K, ♂); Larut, Turu, *King 6751* (CAL, L, P, ♂); Larut, Turu, Gunong Bubu range, *King 7612* (CAL, SING, ♀), *7679* (CAL, K, ♂, ♀); Matang Jambu, *Wray 2528* (CAL, SING, ♀); Teluk Anson, *Allen 37244* (A, BO, K, SING). TRENGGANU: Ulu Brang, *Moysey & Kiah 33745* (SING). PAHANG: Gat, near Raub, *Burkill & Haniff 16929* (SING); Kuala Lipis, *Nong CF 1258* (SING); Temerloh, *Awang CF 2398* (SING), *Kassim CF 0731* (SING, ♂). SELANGOR: Bukit Badat res., Rawang, *Bahsin CF 32403* (SING); Kuala Lumpur, *Hose CF 4599* (K, SING, ♀); Sungei Buloh For. Res., *Hashim 37* (K, ♂); Weld Hills Res., *Hamid CF 4575* (K, ♀). NEGRI SEMBILAN: *Franck 1197* (C). MALACCA: *Alvins 590, 1070, 1234, 1317* (SING), *1624* (SING, ♀), *Maingay 1474* (CAL, K, L, ♂, ♀), *1475* (K), *1476* (CAL, GH, K, L, ♂, ♀); Batu Tiga, *Holmberg 766* (SING); between Roombiya and Aloor Gafah, *Griffith 4664*, Sept. 1842 (K); 14–14½ miles Sungei Udan For. Res., *Sinclair SFN 40597* (K, SING). JOHORE: Gunong Pantai, *Corner s.n.*, Jan. 1937 (SING); Sungei Pelepah Kiri, *Corner s.n.*, June 1937 (SING). PENANG: Government Hill, *Curtis s.n.*, Mar. 1894 (SING, ♀); Penaea Bukit, *Curtis 1984* (SING); Penang Hill, *Nanen s.n.*, June 1940 (SING); Waterfall, *King s.n.*, Aug. 1879 (CAL); Waterfall Quarry, *Curtis 3603* (CAL, K, SING, ♀). SINGAPORE: Changi, *Ridley 3357* (K), *4437* (CAL, SING, ♂, ♀); Garden Jungle, *Ridley 6542* (BM, CAL, K, ♂, ♀).

Sumatra. *De Vriese 23* (L), *De Vriese & Teysmann 18* (L). TAPANULI: Barus, Pardamuan, *bb 31402* (A, BO, L); Padang Lawas, Gunong Tua Djulu, *bb 6443* (BO). WEST COAST: Ayer Waringun, *Burck s.n.*, Aug. 1883 (BO, L); Priaman, *Diepenhorst HB 7292* (BO, P), *Teysmann 754* (BO); Sinkara, *Teysmann HB 756* (BO, CAL, L, U). EAST COAST: Huta Padang, Asahan, *Krukoff 4376* (A, BO, L, SING, ♀); Karolanden, Lao Pengulu, *bb 12503* (BO); Langkat, Sungei Sedapan, *bb 9132* (BO); Tasik, *Koorders 10456* (BO). INDRAGIRI: Keritang, *bb 28660* (BO, L, SING); Kuantan, Djake, *bb 26487, 26491* (BO, L); Kuantan, Sungei Besar, *bb 24028* (BO, L); Peranap, *bb 30102, 30120* (A, BO, L). DJAMBI: Muara Pidjuan, *bb 12273* (BO, L, ♂). BENKULEN: Redjang, Penandjung pandang, *bb 2735* (BO, L). PALEMBANG: *Praetorius s.n.* (L); Banjuasin and Kubustreken, *Grashoff 809* (BO, L); Banjuasin and Kubustreken, Bajunglintjir, *NIFS T 27* (BO, L, ♂, ♀), *195* (BO, K, L, SING, ♂, ♀); Komering Ulu, *Grashoff 575* (BO); Lematang Ilir, Gunong Magang, *NIFS T 284* (BO, L, P, SING, U, ♂, ♀), *300* (BO, L, ♂), *522* (BO, ♂); Lematang Ilir, Semangus, *bb 32245* (BO, L); Muara Dua, *Grashoff 461* (BO, L); Muara Dua, Kisau, *bb 9630* (BO); Muara Mengkulem, *Forbes 3041* (A, BM, CAL, L, P, SING, ♂, ♀); Musi Ilir, Ipil, *NIFS T 1071* (BO, L); Rawas, *Grashoff 1032* (BO, L); Pasemahlanden, Djangkar, *bb 8106* (BO). LAMPONGS: Mangala, *Gusdorf 47* (BO, ♂, ♀), *Teysmann HB 4358* (BO, L, U), *4369* (P), *4393* (BO, L, U), *4419* (BO, U); Seputik, Suwikis, *bb 2844* (BO, L); Seputik, Tulangbawang, Gunong Sugit, *Gusdorf 140* (BO, ♀). SIMALUR: *Achmad 814* (BO); Landschap

Tapah, Defajan, *Achmad 1429* (BO, K, L, U). BANKA: *Teysmann HB 3296* (BO), *6844* (BO, K, L, P); Blinju, *Grashoff 14* (BO, L, ♂, ♀); Blinju, foot of Gunong Rengkuk, *Berkhout 149a* (BO); Djebus, *Teysmann HB 3369* (BO, U), *7243* (L), *7252* (C, L, P); Lobok-besar, *Kostermans & Anta 824* (A, K, ♂); Muntok, Majang, *bb 7596* (BO); Toboali, *Teysmann HB 7265* (BO, P); Tohrin, *sine nom. HB 296* (U). BILLITON: *Rossum 20* (BO, K, L, ♂), *76* (BO), *Teysmann HB 17580, 17583* (BO); Tandjong Pandjang, *bb 6778* (BO). RIOUW ARCHIP.: Tandjong Pinang, Bintan, *Teysmann HB 7284* (BO, C, L, P). LINGGA ARCHIP. NIFS Ri./I–128 (BO). P. Singkep: Marok Tuwa, near Sungei Lorong, *Amat 12* (L); Ulu Sungei Marok Tuwa, *Amat 34* (BO, L).

Borneo. SARAWAK. *Beccari PB 2478* (K, P, ♂), *2998* (K, P, ♀); near Kuching, *Haviland 1888* (CAL, K, ♀); Mt. Poi, *Clemens 20305* (K, NY); Sibu Sungei Assan, *For. Dept. Sarawak S 0502* (SAR). WEST BORNEO. Melawie, Tjatit B. Tangkujung, *bb 26439* (BO, L); Sadakan, Pait, *bb 8048* (BO, L). SOUTH AND SOUTHEAST BORNEO. Martapura, Djungur, *bb 10384* (BO); Pleihari, Sungei Sangga, *bb 9950* (BO); Tanah Bumbu, Kampong Baru, *bb 13356* (BO, L, ♂, ♀). EAST AND NORTHEAST BORNEO. E. Kutei: Sangkulirang, Ranggang, *bb 7968* (BO); Tandjong Bangko region, mouth of Mahakam River, *Kostermans 7186* (K, L, ♀). W. Kutei: Djembajan, Sungei Kelasan, *bb 25122* (BO, L); Djembajan, Sungei Gitan, *bb 12766* (BO); Tandjong Tsue, *Endert 1953* (A, K, L). BRITISH NORTH BORNEO. Elphinstone prov., Tawao, *Elmer 21514* (A, BM, BO, C, GH, K, L, P, SING, U, ♀). P. LAUT. Sungei Paring, *bb 12897* (BO, U, ♂, ♀), *13258* (BO).

Java. *Blume 1364* (CAL, L, ♀), *Reinwardt s.n.* (L), *De Vriese 1655* (L). WEST JAVA. Batavia: Depok, *Beumée 6021*, *Hallier s.n.*, Aug. 1896 (BO), *Koorders 31077* (BO, L), *41048* (BO, ♀), *42776* (BO), *42792* (BO, ♂), *44119* (BO), *Van Steenis 12750* (L); between Kota Bambu and Djembatan duren, *Backer s.n.*, 1902 (BO, ♂); Leeuwiliang, Pasir Angsana, *Bakh. van den Brink 6974* (BO, K, L, ♂, ♀); Leeuwiliang, Pasir Tjihideung, *Bakh. van den Brink 6386* (BO, L); Leeuwiliang, Tjibata, *Bakh. van den Brink 6796* (BO, L, ♀); Tjiampea, *Koorders 30364*, *30365* (BO), *30366* (A, BO, L, ♂). Buitenzorg: Handjere, Janglappa, *NIFS Ja 6206* (L). Cheribon: Kuningan, *Houter 67*, *138* (BO). Preanger: Palabuanratu, *Koorders 8738* (BO, L), *12561*, *12562* (BO, L, ♂), *12570* (A, BO, L, P, ♂, ♀), *15677* (BO, L, ♂), *33049* (BO); Palabuanratu, Buniwangi, *sine nom. et num.*, Mar. 1873 (BO); Palabuanratu, Tjibareno, *Winckel 1858* (BO, L, U, ♀); Sanggrawa, *Koorders 8739* (BO). CENTRAL JAVA. Pekalongan: Loutresten, E. Tegal, *Beumée 1889* (BO); Pemalong, *Bruscomps 8* (BO). NUSA KAMBANGAN: Tjilatjap. *Koorders 27032* (BO, ♀). **Lesser Sunda Islands.** Bali: [? cult.] *sine nom. et num.* (L).

Cultivated. INDIA: Calcutta, Hort. Bot., *Wallich 2142* (P), *4658D* (BM, CGE, K), *s.n.*, 1819 (BM, ♂, ♀). JAVA: Bantam, *Zollinger 1009* (A, L, P, U); Bogor, Hort. Bot., *Zollinger 2982* (BM, P, U, ♀). Unlocalized collections: *Abel s.n.* (East Indies) (K, ♀); *Kurz 2084* (CAL); *Roxburgh s.n.* (BM).

The synonyms given above all refer exclusively to *Artocarpus rigidus* ssp. *rigidus*, as do the references, except for King's descriptions (1888, 1889) which include *A. hispidus*. Merrill (Jour. Arnold Arb. 19: 331. 1938) reduced *A. rigidus* to *A. rotunda* (Houtt.) Panzer, Pflanzensyst. 10: 380. 1783, based on *Rademachia rotunda* Houtt. Nat. Hist. II. Pl. 11: 455. 1779, which was very briefly described from Javan material as having leaves of the same shape as *Artocarpus integer* but without "roughness"

except on the fruit, which was round and grew, so Houttuyn was told, to the size of a child's head. This could be a crude description of *A. rigidus* but, in fact the leaves in this species are more or less scabrid beneath, the twigs and peduncles are appressed-hispid and the syncarp is smaller. Since no type has been found at Leiden, the identification would have to be based primarily on the vernacular name *Mandelique* given by Houttuyn, which is cited by Teysmann and Binnendijk (Cat. Bog. 85. 1866) and by Koorders and Valeton (1906) as a Javan name for *A. rigidus*. The description does not fit any other species occurring in Java and it seems preferable to treat *A. rotunda* as a *nomen dubium*.

The specimen listed above from Bali is probably from a cultivated tree, since there are no other records of *A. rigidus* from eastern Java or the Lesser Sunda Islands as an indigenous plant. One of the collections from Penang, *Curtis s.n.*, May 1894, has the syncarp processes softly pubescent, but otherwise agrees with *A. rigidus* ssp. *rigidus*.

ssp. **asperulus** (Gagnep.) Jarrett, stat. nov.

Artocarpus calophylla Kurz, Prelim. Rep. For. Pegu App. A, 124, App. B, 82. 1876, in clavis, For. Fl. Burma **2:** 431. 1877, non Teysm. & Binnend., 1866, quae est nomen nudum; King in Hook. f. Fl. Brit. Ind. **5:** 540. 1888; King, Ann. Bot. Gard. Calcutta **2:** 8. *t. 2.* 1889. Holotype, Burma, *Kurz s.n.* (CAL).

Artocarpus asperula Gagnep. Bull. Bot. Soc. Fr. **73:** 86. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. **5:** 734. *fig. 90.* 1928. Syntypes, Indochina, *Chevalier 30083*, *Herb. For. Cambodge 36930*, *Pierre 15*, *1851*, *Poilane 6644*, *Thorel 1067* (P); lectotype, *Poilane 6644* (P).

Artocarpus asperula var. *hirta* Gagnep. Bull. Soc. Bot. Fr. **73:** 87. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. **5:** 735. 1928. Syntypes, Indochina, *Pierre 3377*, *3777*, *Thorel s.n.*, 1862–66 (P); lectotype, *Pierre 3777* (P).

Artocarpus chaplasha auct. non Roxb., Gagnep. in Lecomte, Fl. Gén. Indoch. **5:** 735. 1928.

Differs from ssp. *rigidus* as follows: *twigs* rather softly and densely subappressed hispid-pubescent, juvenile shoots with long patent hairs; *leaves* obovate-oblong to ovate, base rounded or shallowly cordate, rarely cuneate; very shortly appressed-hispid above, rarely nearly smooth, indumentum beneath as on shoot; lateral veins 9–12 pairs; *syncarp* with processes hispid from spreading hairs c. 0.5 mm. long.

VERNACULAR NAMES: *Taung peing*, Burma; *Kanun pan*, Siam; *Knol prey* or *Knor prey*, Cambodia; *Cay mit nai* or *Mit nai*, Annam. USES: as in ssp. *rigidus*.

DISTRIBUTION: in evergreen forest to 3000 ft., Burma, Siam, Indochina.

Burma. Kyauktwin [not located], *Meebold 15599* (CAL). TENASSERIM. Amherst: *Falconer 1015* (CAL, ♀); Mekhrein chaung, *Parkinson 5205* (DD, ♀); Moulmein, *Kurz s.n.* (CAL). Tavoy: Kalemaung Res., *Ba-Pe 864* (CAL, DD, ♀); Kadwe For. Circle, *Manson 762* (CAL, ♀). **Siam.** Chanburi [Chantaburi ?], Makham, Khao sabap, *Put 2368* (CGE); Rayawng, Ban Pe, *Kerr 2734* (BM, ♀); Kaw Chang (island off se. coast), Klawng Mayom, *Kerr 6923* (BM, P, ♀), *Marcan 1329* (BM, ♀). PENINSULAR SIAM. Surat, *Sman 2365* (CGE, ♂, ♀); Surat,

Panom, *Kerr 12375* (BM, ♀). Island off w. coast: P. Terutao, *Kerr 14198* (BM, ♀). Islands off e. coast: Kaw Pa-ngan, *Kerr 1235* (BM, ♀); Kaw Tao, *Kerr 12799* (BM, K, ♂).

Indochina. CAMBODIA: *Hahn 61* (P); Kamput, *Pierre 15* (P); Phom-ba, Nem-Tram-Kok, *Müller 350* (P); Pursat Prov., Pnom Barong, Roleap, *Herb. For. Cambodge 36930* (P). COCHINCHINA. *Thorel 1067* (A, BM, K, P, ♂, ♀), *Thorel s.n.*, 1862–6 (P). Baria prov.: *Chevalier 36637* (P), *Commission de la Gutta 4* (P); Xuon moc, Chevalier *36606* (P, ♀). Bien Hoa prov.: *Commission de la Gutta s.n.*, 1866 (P); Bao Chiang, *Pierre 1851*, p.p. (A, BM, K, P, ♀); Song lu, *Pierre 3777* (A, P); Trang-bom, *Chevalier 30083* (P, ♀), *Chevalier 36761* (P), *Fleury 39323* (P, ♀). Budot, *Müller 1728* (P). Saigon [? cult.], *Pierre 3377* (P, ♀). Tay ninh prov., Cay Cing, *Pierre 1851*, p.p. (L). ANNAM: Massif de la Mère et l'Enfant, *Poilane 6644* (K, P, ♀). P. CONDORE: *Perry 4699* (P).

This subspecies is consistently distinguished from the type by the hispid and not hispidulous syncarp processes, and usually also by the rounded or shallowly cordate base and rough upper surface of the leaves. In indumentum and leaf shape it is rather variable, though the hairs are usually denser and softer on both shoot and leaf than in ssp. *rigidus*. The latter feature is most marked in Burma, where, in addition, the leaves are frequently ovate. This form was described by Kurz as *A. calophylla* and is shown in King's plate (1889), drawn from *Falconer 1015* and not Kurz's own collection, as stated by King, who reversed these two collections in his discussion of the species. In Siam and Indochina the leaf shape is usually obovate-oblong and the form was described by Gagnepain as *A. asperula*. However, since the variation between the two forms is continuous, they are here united. Both species were distinguished by their authors from *A. rigidus* by the indumentum of the leaf, but, since the differences in this and in the leaf shape are not constant and those in the syncarp are so slight, it is preferable to treat the continental entity as a geographical subspecies of *A. rigidus*. The northern boundary of Malaya appears to separate the two subspecies, with the exception of Helfer's collection of ssp. *rigidus* from Tenasserim, but more material from this area is desirable to show whether there is any intergrading of characters.

Gagnepain's *A. asperula* var. *hirta* was described from sapling collections with long patent hairs on the shoot. Two Indochinese collections of *A. rigidus* ssp. *asperulus* at Paris, *Comm. de la Gutta s.n.*, 1866, and *Pierre 15*, were labelled *A. polyphema* Pers., but the native species which may have been included by Loureiro in his confused description of *Polyphema champeden*, on which this name is based, is not identifiable, although it will be further discussed under *Artocarpus integer*. The identification was not mentioned by Gagnepain in 1928.

(*To be continued*)

A YELLOW-FLOWERED FORM OF RHODODENDRON CAROLINIANUM

LEONARD F. FRISBIE

Rhododendron carolinianum Rehder f. **luteum**, forma nova.

A low, evergreen shrub of medium-compact growth. Branchlets brown with scattered scales. Leaves lanceolate, acuminate to acute at the apex, cuneate at the base, the blade to 6.3 cm. long, 2.5 cm. wide, yellowish green, glabrous above, reticulate, densely scaly below with scales separated by one-half their width, the petioles to 1.2 cm. long, scaly. Inflorescences terminal, the rachis 2 cm. long, about 6-flowered, the pedicels about 1 cm. long, scaly. Calyx-lobes 5, ca. 2.7 mm. long, scaly; corolla rotate-funnel-shaped, 4 cm. across, mimosa yellow [Horticultural Color Chart 602/1], nearly self-colored, scaly on the outside, the lobes obtuse, the tube 1.0 cm. long; stamens 10, ca. 1.5 cm. long, slightly exserted, hairy at the base; ovary oblong, ca. 1 cm. long, scaly; style glabrous. Capsule narrowly oblong, 1.3 cm. long, scaly.

Frutex humilis sempervirens, compacto-mediocriter incremens. Ramuli fusci squamis sparsis. Folia lanceolata, acuminata vel acuta, basi cuneata, lamina 6.3 cm. longa, 2.5 cm. lata, flavo-viridia, reticulata, dense squamosa. Inflorescentia terminalis, rachis 2 cm. longus, sex-floribus intextus; pedicelli ca. 1 cm. longi; corolla rotato-infundibuliformis, 4 cm. lata, "mimosa flava," prope uniformiter colorata, extus squamosa, lobis obtusis, tubulo 1.0 cm. longo; stamina 10, ca. 1.5 cm. longa, parum exserta, basi pilosa; ovarium squamosum, stilus glaber. Capsula 1.3 cm. longa, squamosa.

TYPE: Plant in cultivation, 2728 Lemons Beach Road, Tacoma 66, Washington; known only to have come from "the mountains of western North Carolina," *L. F. Frisbie*, May 15, 1958 (Herb. Arnold Arboretum).

This very handsome and distinctly different color-form of *Rhododendron carolinianum* was one of a group of native plants obtained about 1945 by Halfdan Lem of Seattle, Washington. The plants were offered to Mr. Lem as being "yellow-flowered carolinianum." He accepted the small plants, but had such small faith in the possibility of the claim that he promptly forgot about the plants in the press of other matters. In the spring of 1957 this writer on a visit to Mr. Lem's garden was attracted by one of the plants in flower. Due to my keen interest Mr. Lem let me have the form and it was brought to Tacoma. Subsequent efforts to gain information as to the exact natural location of the plants have met with no success. The possible collectors whom we have contacted have all given negative answers, and seemed to know nothing of such a form of the species, so it has proved impossible to obtain more exact information than that given above.

At the present writing the plant is thriving, is making excellent growth, and has adapted itself very well to this climate. It will make an excellent

addition to the series of evergreen rhododendrons, and will be a valuable horticultural subject wherever rhododendrons are grown. Here in western Washington, where a wide range of types of the genus is grown, we are very much pleased with this new color form. The hybridizing potential of the *luteum* form is intriguing, especially so in the light of such acceptable hybrids of the typical form as 'Conewago' and 'Conestoga.'

This yellow-flowered form of *Rhododendron carolinianum* is being propagated by ground layering and every effort will be made to see that it is generally available through the Washington Rhododendron Society, Inc.

In addition to this color variation the typical form of the species with clear pink flowers is highly valued for decorative garden purposes, and a special place is reserved for the white-flowered form, *R. carolinianum* var. *album* Rehder. Good foliage, compact habit, and free flowering with chaste trusses of multiple flowers make this form a favorite which sometimes wins in rhododendron shows over all other species exhibited. The three color forms of *Rhododendron carolinianum* make a delightful combination in the garden, a grouping of true distinction. But we have found that it pays to be selective, especially with the pink and white forms of the species. Collected plants are not difficult to obtain, and persistent culling will turn up a very few plants of outstanding quality. Here in the West where the genus grows so well, some shaping and pruning are essential if one is to have compact plants.

These distinctive forms of native American rhododendron species, both evergreen and deciduous solidly substantiate the importance of the work of the selective collector, a field in which the Washington Rhododendron Society has made a notable contribution.

2728 Lemons Beach Road
Tacoma 66, Washington

ANDRODIOECISM IN THE FLOWERS OF TROCHODENDRON ARALIOIDES

HSUAN KENG *

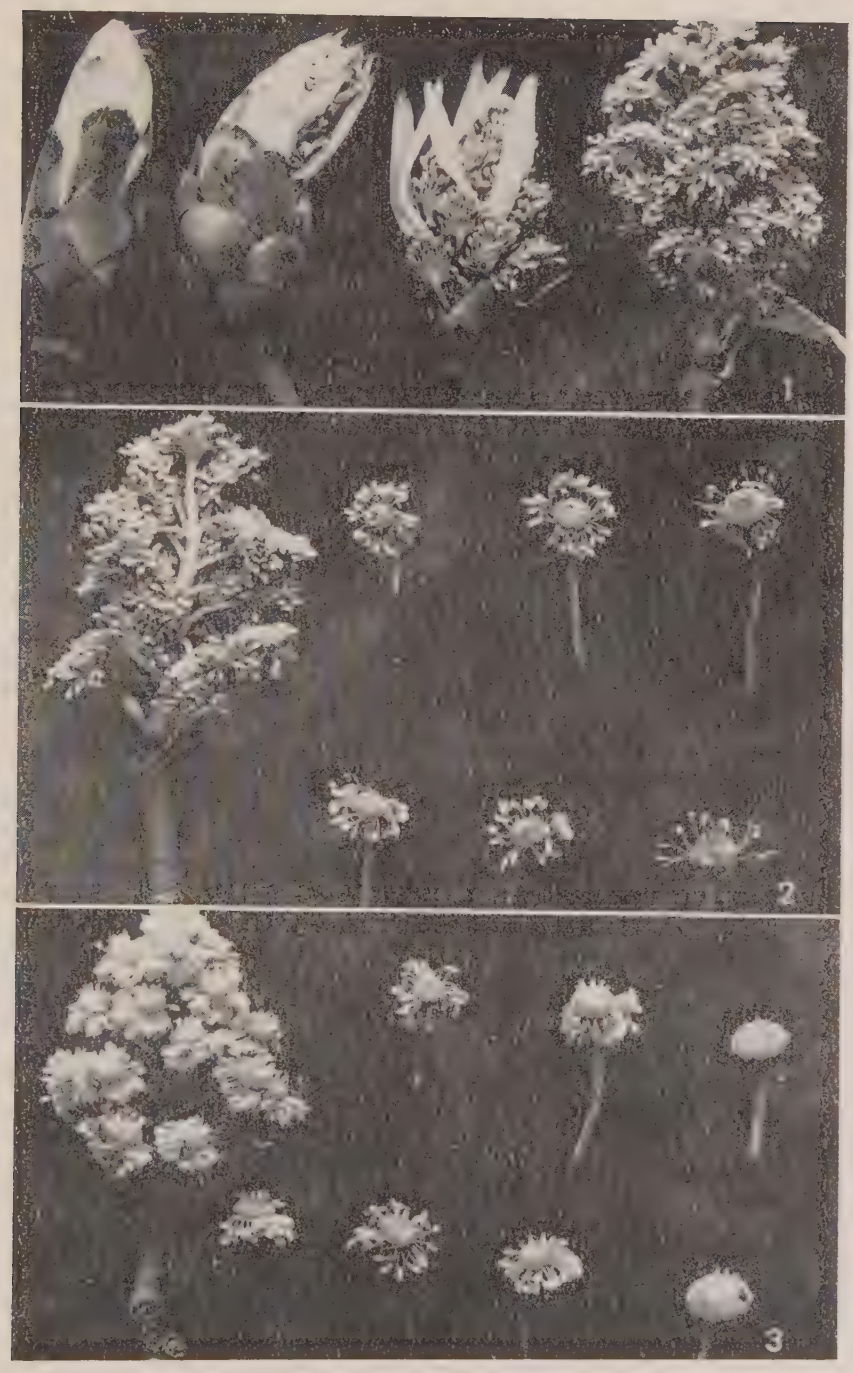
EXISTING DESCRIPTIONS of *Trochodendron aralioides* Sieb. et Zucc., the sole living representative of the vesselless angiospermous family Trochodendraceae (Smith 1945, Lawrence 1951), are based primarily on herbarium specimens. In all the botanical works consulted the flowers are described as hermaphrodite. The literature is reviewed in detail by Smith (1945).

In the spring of 1957, from January to June, the author visited Bamboo Lake, forty miles northwest of Taipeh, Formosa, every two weeks to collect flowering buds, flowers, and fruits of *Trochodendron*. A number of trees growing naturally in the valley and on the hill slopes were examined. About half of them were found to be protandrous: during the maturation of the stamens, the styles are clasped together (*Figs. 1, 2*). The other half were found to be protogynous, with the styles recurved distally, exposing the ventral stigmatic surfaces, at a time when the stamens had not yet dehisced (*Fig. 3*). All the flowers of any one tree without exception presented the same condition, *i.e.*, they were either all protandrous or all protogynous.

In mid-April the trees were in full bloom and were being frequented by honey bees (*Apis mellifica, A. indica*) and snake-eyed butterflies (*Ypthima motschulski*). The carpels and filaments of open flowers are pale yellowish green, while the anthers are bright yellow in color. A shining, viscid fluid coats the external surface of the gynoecia in a great majority of both protandrous and protogynous flowers, although no nectar has been found. The sweet, pleasant fragrance is detectable from some distance away, especially on a sunny morning. Occasionally a few flowers appear to lack a coating of viscid fluid and remain dry.

In protogynous flowers the stamens possess well developed anther-sacs which dehisce subsequently to release normal pollen. In addition, the gynoecia are also well developed. On the other hand, in protandrous flowers, with an equally normal androecium, the styles are at first tightly clasped, only opening slightly later. The trees which bear protogynous flowers produce normal follicles and fertile seeds. However, the author failed to find a single normal follicle on those trees which bore protandrous flowers. Thus, the species appears to be androdioecious, a condition which Darwin (1896, p. 13) pointed out as being exceedingly rare among flowering plants. It would be most interesting to have reports on the floral biology of *Trochodendron* from other parts of its range, particularly from the islands of Japan.

* The author wishes to express his thanks to Dr. Lincoln Constance and Dr. Herbert G. Baker for their helpful suggestions.



Trochodendron aralioides Sieb. & Zucc.

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EXPLANATION OF THE PLATE

FIG. 1. Stages in the unfolding of the inflorescence of *Trochodendron.* FIG. 2. Development of protandrous flowers. FIG. 3. Development of protogynous flowers. (All natural size.)

THE EMPETRACEAE AND DIAPENSIACEAE OF THE SOUTHEASTERN UNITED STATES

C. E. Wood, Jr. and R. B. Channell

The studies of Empetraceae and Diapensiaceae, two small families of both biosystematic and phylogenetic interest considered below, are part of a generic flora which is in preparation for the southeastern United States.[1] The genera of these families provide examples on a different level of complexity from those of nine families of Ranalian affinities, the treatments of which have been published previously (Jour. Arnold Arb. 39: 296–346. 1958; 40: 94–112. 1959). Further examples of the diversity of the plants of this area and of the problems which they present will be published as space permits in order that some of this material may be

[1] Preliminary to a manual of the species of seed plants of this area, generic treatments of this type are intended to call attention to problems of various kinds which will require the talents of all available workers before it will be possible to understand thoroughly the plants of this large area; to bring together a large part of the information available concerning the genera which occur there; to focus attention where possible on the biosystematic aspects of each group; and to examine and clarify the confused generic lines so often found among groups of plants in the southeastern United States. Although to some the approach from the generic level may seem a roundabout one, we are confident that, by bringing together in one place information of the kind presented in the treatments below, the widest interests of taxonomy and taxonomists will be served in both research and teaching and that the ultimate goal of an understanding of the plants of the area will be reached more quickly through this approach than through the traditional one.

While one may speak of "alpha" and "omega" taxonomy and insist that one precede the other, in times such as the present with the ever increasing destruction of the natural areas of the earth — a process all too evident in the southeastern United States — it is important as never before that taxonomic problems be approached simultaneously on all levels, from the alpha to the omega, and from all directions, and that the taxonomist have the knowledge and viewpoint to do this. It is not sufficient to say "Collect now — study later." The very items the monographer or careful student of evolution may need to know are the ones which may easily be overlooked (and often are) by the well-meaning but uninformed collector. Provided with a guide to some of the critical features which need observation, with some idea as to the basis of the taxonomic complexities of a group, or with a knowledge of the gaps in the information available concerning a group of plants, a worker is in a much more favorable position to obtain critical information in the field, and to look at plants with an awareness which is lacking among those whose aim is only to collect and identify. If taxonomy as a science is to command the respect of workers in other disciplines, if it is to be both analytic and synthetic, and if a modern flora of any area is to have a firm basis in an understanding of the plants involved, the approach must be one of understanding plants as living organisms and the information considered must come from all branches of botany and from all levels — from the alpha to the omega. Generic treatments of the kind presented here may serve the interests of workers on any of these levels. Certainly a number of taxonomic and phylogenetic, as well as morphological and biological, problems will be apparent to the thoughtful reader of the descriptions, notes and references which follow. — C. E. W.

made more immediately available to those interested in the plants of eastern North America.

The general scheme of these studies is outlined in the first paper of this series (see above). It should be pointed out again, however, that the southeastern United States as defined here is bounded by and includes North Carolina, Tennessee, Arkansas and Louisiana; that the descriptions are based primarily upon the species occurring within our area, any supplementary material added for clarity being included in brackets; that the abbreviations used for periodicals are the very useful ones of Lazella Schwarten and H. W. Rickett (Abbreviations of titles of serials cited by botanists. Bull. Torrey Bot. Club 76: 277–300. 1958); and that references which we have not seen are marked by an asterisk. All of this work, which is being conducted as a joint project of the Gray Herbarium and the Arnold Arboretum, has been made possible through the kind support of George R. Cooley and through a grant from the National Science Foundation.

The detailed drawings of the four genera are the careful work of Dorothy H. Marsh. We are indebted to H. L. Blomquist, of Duke University, and to R. K. Godfrey, of Florida State University, for their respective kindness in sending for study and use in illustration a large series of specimens of *Pyxidanthera brevifolia* and excellent fresh specimens of *Ceratiola* in fruit.

EMPETRACEAE (Crowberry Family) [2]

A small family of evergreen shrubs of ericoid habit with numerous pulvinate leaves, inconspicuous apetalous flowers of few stamens and drupaceous fruits. Three genera of disjunct distribution and about eight species: *Empetrum L.*, bicentric, with about four boreal species, primarily of arctic to subalpine distribution, and a single species in the subantarctic; *Corema* D. Don, with *C. Conradii* (Torrey) Torrey ex Loud., in widely separated areas from the Magdalen and Prince Edward islands and Nova Scotia to New Jersey, and *C. alba* (L.) D. Don in Portugal and the Azores; and the monotypic *Ceratiola* Michx. confined to our area.

The systematic position of the Empetraceae has been the subject of considerable controversy. The family has been variously allied with the Celastrales, Ericales and Sapindales. The erect ovule and ventral raphe have been considered to indicate affinities with the Sapindales. A natural group, it is perhaps best regarded as a reduced apetalous and polygamous or dioecious derivative of the Ericaceae. This view is supported by the embryological data of Samuelsson and is confirmed by the morphological studies of Hagerup. A whole series of well-marked embryological features characterizes the Ericales. These represent standard stages in Ericalean embryology and constitute a combination unknown in any other order. The Empetraceae show close correspondence in all respects. The embryol-

[2] By R. B. Channell.

ogy of the Celastrales and Sapindales differs in so many ways as to render any link with the Empetraceae obscure indeed. The 3-colporate pollen grains are united in tetrahedral tetrads as in Ericaceae.

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1. **Ceratiola** Michx. Fl. Bor.-Am. **2**: 221. 1803.

Dioecious shrubs of dry sand strands and sand hills, emitting a characteristic odor. Leaves linear-acicular, in "decussate" whorls, with a longitudinal groove on the lower surface, jointed at the base of the short petiole. Old stems roughened by petiolar sterigmata. Flowers axillary, sessile, hypogynous, the perianth consisting of 5–6 bracts and sepals. Male flowers of 2 exserted stamens, the 2-loculed anthers longitudinally dehiscent; pollen in tetrads. Female flowers with a single pistil, the 3–4 exserted stigmas divergent, flabellate-incised-pinnatifid, united into the single style arising from the summit of the ovoid, 2-locular ovary. Fruit small, greenish-yellow, drupaceous with 2 pyrenes, the seeds with a straight embryo. Type and sole species: *Ceratiola ericoides* Michx. (*C. falcatula* Gandoger, *Empetrum aciculare* Bertol.) (Name from Greek *ceras*, horn, apparently alluding to the flabellate style-branches.) — Rosemary.

Often covering extensive areas, *Ceratiola* is associated with pines and oaks throughout its range from Florida to South Carolina and Mississippi, and is a more or less characteristic shrub of the *Pinus clausa*-scrub in Florida. It does not occur on the Florida Keys. In some areas, especially on coastal sand dunes, it is associated with a shrub of similar habit and stature, *Solidago* (*Chrysoma*) *pauciflosculosa* Michx. Inhabiting extremely dry situations in pinelands, in sand hammocks and on inland sand dunes, often in almost pure sand with *Selaginella arenicola* Underw. and *Cladonia*,

Ceratiola is often ravaged by fire. In southern Florida it may be seriously parasitized by the lauraceous woevine, *Cassytha filiformis* L.

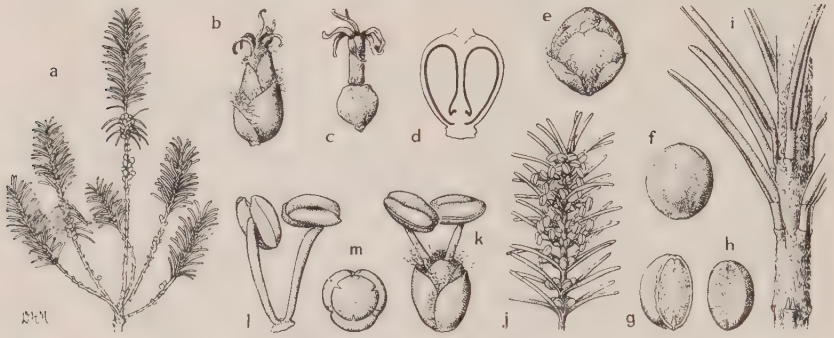

FIG. 1. **Ceratiola.** a–m, *C. ericoides*: a, habit, ♀ plant, × ½; b, ♀ flower, × 6; c, pistil, × 6; d, young ovary, semi-diagrammatic vertical section, showing two locules each with a single ascending ovule, × 12; e, mature fruit inclosed in weathered bracts and sepals, × 6; f, mature fruit free of bracts and sepals, × 6; g, pyrene inclosed in ovary wall, × 6; h, pyrene, × 6; i, portion of vegetative shoot showing position and arrangement of leaves — note articulate, pulvinate, appressed petioles, × 6; j, portion of ♂ shoot in flower, × 1; k, ♂ flower, × 6; l, stamens of a single ♂ flower, × 6; m, pollen tetrad, ca. 30 μ diameter, × ca. 300.

Usually a well-formed shrub, *Ceratiola* is very exacting in habitat and, like *Empetrum* and *Corema*, is difficult to cultivate, presumably because of a mycorrhizal relationship. The common name rosemary refers to the superficial resemblance to *Rosmarinus officinalis* L.

Little is known concerning the agent of pollination (wind?), germination and other biological features of the species.

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DIAPENSIACEAE (DIAPENSIA FAMILY) [3]

Low, evergreen herbs or subshrubs of acid soils, tufted or creeping, with simple exstipulate, alternate leaves. Flowers regular, the sepals 5, free, imbricate, the petals 5, separate or united, the corolla campanulate or funnel-shaped. Androecium typically of two whorls: an outer of 5 connivent fertile stamens, and an inner (when present) of 5 staminodia oppo-

[3] By C. E. Wood, Jr.

site the petals; filaments adherent to the petals (and sometimes monadelphous, as well); pollen grains single, 3-colporate. Style simple, the stigma 3-lobed, the ovary 3-loculed, superior, lacking a disc at the base; ovules 2-integumented, the placentation axile. Fruit a loculicidal capsule; seeds as in Ericaceae. (Including Galacaceae of Small's Manual.)

A small family of five genera, primarily of eastern America and eastern Asia (with the exception of the circumpolar *Diapensia lapponica* L.), forming a natural group with numerous reticulate relationships. Two tribes, Diapensieae Gray and Galacineae Gray, generally are recognized, although variously delimited (see Gray, Drude, Diels).

The group is usually agreed to be related to the Ericales but differs from most in the simple pollen grains, the epipetalous stamens and the absence of a disc. In view of the importance accorded embryological evidence in allying the Empetraceae with the Ericales it should be noted that the embryological features of *Diapensia lapponica* do not fit with those of other members of the Ericales. Further embryological studies of other genera are highly desirable. The family is currently placed either with the Ericales or in a separate order Diapensiales. Chromosome structure and basic number are similar throughout those members of the family thus far examined. The stamens and staminodia present interesting problems in function and morphology.

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Key to the Genera of Diapensiaceae

A. Plant with small awl-like leaves; prostrate, creeping; staminodia lacking; anthers 2-locular, apparently transversely dehiscent, each locule awned on the lower side; capsule with a persistent but easily broken columella. . . . . 1. *Pyxidanthera.*

A. Plant rhizomatous with shining oval to orbicular leaves; 5 staminodia present.
  B. Flowers large, solitary; petals connate, crenate-undulate-toothed; anthers large, oval, 2-locular; staminodia distinct, near base of corolla; capsule with a persistent columella; seeds ovoid or spherical. . . . . 2. *Shortia.*

B. Flowers small, numerous, in wand-like racemes on naked scapes; petals entire, distinct; stamens and staminodia monadelphous, forming a tube adnate to the petals; anthers 1-locular; capsule without a columella; seeds angular. ..... 3. *Galax.*

1. **Pyxidanthera** Michx. Fl. Bor.-Am. 1: 152. *pl. 17.* 1803.

Creeping, prostrate, evergreen subshrub from a woody root, the small leaves alternate, oblanceolate, awl-pointed, sessile and hairy on the upper side (at least near the base). Flowers solitary and sessile on short, densely leafy branches. Sepals concave, oblong, reddish. Corolla white, about 5–10 mm. broad, the petals united by the broad stamen-filaments to form a tube, the lobes broadly spatulate, cuneate or obovate-cuneate. Stamens alternating with the petals, the filaments white, almost petal-like, the anthers bent inward; anther locules 2, each apparently dehiscing transversely and awned at the base; staminodia lacking. Style as long as the corolla tube, increasing somewhat in length in age; ovules 4–6 in each locule of ovary. Fruit with a persistent but brittle and easily broken columella; seeds globular, regularly pitted (seldom collected). $2n = 12$. TYPE SPECIES: *P. barbulata* Michx. (Name from the Greek *pyxis*, a small box, and New Latin *anthera*, for anther, from the appearance and dehiscence of the anthers.) — PIXIE, FLOWERING-MOSS.

One or two species: *Pyxidanthera barbulata*, of sandy pine barrens, usually seasonally wet, on the coastal plain from New Jersey to Virginia, and North and South Carolina, and *P. brevifolia* Wells, of the inner coastal plain, Harnett Co., N. C. to Darlington Co., S. C. The status of this second species, which is associated with *Quercus laevis* Walt. and *Pinus australis* Michx. f. on the rolling sand hills, needs careful study, for it appears to intergrade in moister habitats with the more widespread plant. Although *P. brevifolia* when well developed is characteristic in aspect, its only distinctive features are the smaller size of all parts and the greater hairiness of the leaves and stems, characteristics which may well be attributable to the more xeric habitat and which are matched or approached by various smaller specimens from New Jersey and North Carolina.

The mechanical operation of the awned, connivent anthers, which are apparently transversely dehiscent, is probably significant in the biology of the small, white flowers which are borne abundantly in March and April. Pollen is not discharged from the anther unless the awned tip is pushed downward. A comparison with the stamens of *Diapensia* suggests that the orientation of the anther-locules has changed from vertical to horizontal in the inwardly bent anthers of this plant so that the dehiscence is not truly "transverse."

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2. **Shortia** Torrey & Gray, Am. Jour. Sci. Arts I. **42**: 48. 1842; II. **45**: 402. 1868, nom. cons.

Low, evergreen, perennial herb, forming dense clumps or carpets, the foliage combining the aspect of *Galax* and *Pyrola*. Plants spreading by horizontal rhizomes bearing clustered long-petioled, broadly elliptic to sub-orbicular truncate-emarginate, cordate, lustrous leaves, toothed along the margin, and much smaller leaves or scales. Flowers 2–3 cm. high, solitary on bracted peduncles, nodding. Sepals ovate, imbricate. Corolla open-campanulate, white, pale pink or pale blue, the petals united, the lobes undulate-crenate notched. Fertile stamens with conspicuous, 2-loculed anthers bent sharply inward and connivent in the tube; staminodia borne near the base of the corolla and incurving over the ovary. Style elongate; capsule globular, 3-valved and with a persistent columella bearing the globular or ovoid seeds. $2n = 12$. (*Sherwoodia* House; not *Shortia* Raf., 1840, nom. rejic.) Type species: *Shortia galacifolia* Torrey & Gray. (Dedicated to Charles Wilkens Short, 1794–1863, of Kentucky, "whose attainments and eminent services in North American botany are well known and appreciated both at home and abroad.") — Shortia, Oconee-bells, Little coltsfoot.

In North America a single species and in Japan, Formosa and China perhaps 9–11 species, depending upon specific and generic concepts. *Shortia galacifolia*, *S. uniflora* Maxim., of Japan, and *S. sinensis* Hemsl. form a closely related group of species with solitary flowers and staminodia. Other species with several-flowered inflorescences and partially developed, although sterile, stamens have been treated as the genus *Schizocodon* Sieb. & Zucc., while four species described from Formosa with several-flowered inflorescences and no staminodia would be placed in *Shortiopsis* Hayata. All of these species appear to be closely related, however, and are best treated as a single genus, *Shortia*. The nearest ally is the Sino-Himalayan *Berneuxia* Decne.

Shortia galacifolia, a handsome plant with an intriguing history shares in our area the special fame of *Franklinia* and "Bartram's Ixia" (*Sphenostigma coelestinum* (Bartr.) R. C. Foster). Collected by André Michaux in the Carolina mountains in 1787, the specimen was seen by Asa Gray in Paris in 1839 and was later described as a new genus. All searches for the plant were futile, but a second species described from Japan was recognized by Gray as belonging to the genus. *Shortia galacifolia* finally was rediscovered by George M. Hyams, in McDowell Co., N. C., in 1877, and, in 1886, was found by Sargent and Boynton near the junction of the Horsepasture and Toxaway Rivers in Oconee Co., S. C.

The plant is now known from two limited areas some 60 miles apart: var. *galacifolia*, primarily in the drainage of the Keowee River in Oconee and Pickens counties, S. C., Rabun Co., Ga., and Transylvania Co., N. C., and var. *brevistyla* P. A. Davies, in McDowell and Burke counties, N. C.

FIG. 2. DIAPENSIACEAE. a–h, **Shortia.** *S. galacifolia*: a, habit, × ¼; b, flower, × 1; c, lateral view of flower, corolla removed to show calyx and bracts, × 1; d, opened corolla, × 1; e, stamen, lateral view, × 4; f, staminodium, × 6; g, ovary, vertical section, semi-diagrammatic, × 4; h, ovary, cross section, × 4. i–q, **Pyxidanthera.** i–p, *P. barbulata*: i, habit, branchlet from above, × 1; j, flower, × 4; k, tip of flowering branchlet with flower after fall of corolla, × 4; l, opened corolla, × 4; m, stamens, × 10; n, immature fruit with calyx (2 lobes removed), × 4; o, ovary, cross section, × 10; p, seed, × 20. q, *P. brevifolia*: opened capsule from above, showing persistent but easily dislodged columella in

The two varieties differ in petal-length, -notching and -venation, length of staminodial hairs and length of styles. The ratio of length of style to length of mature ovary is 1:2.4 in the Keowee area and 1:1.3 in McDowell County. On this and other bases it appears that Michaux' specimen came from near the spot where Sargent and Boynton first found it.

Shortia is still abundant in a part of the Keowee area but should be protected from vandalism and excessive commercialism. It occurs in moderately acid soils with good aeration and usually with abundant moisture, growing best under *Rhododendron maximum* or *Tsuga*, but often in association with *Pinus Strobus*, *P. rigida*, *Liriodendron*, *Liquidambar* and *Kalmia latifolia* and various other Ericaceae. The altitudinal range is from about 600 feet (180 m.) to well above 1600 feet (500 m.) but the plant is hardy far to the north of its restricted range. The proterogynous flowers are borne in March and early April and the seeds mature from late April to May (or June). It has been suggested that the restricted distribution is related to the lack of a dispersal mechanism and to limited reproduction by seeds, for the seeds often germinate even within the capsule. However, natural reproduction by seeds is reported in Amherst Co., Virginia, and in the Keowee region.

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center, × 4. r–x, **Galax.** *G. aphylla*: r, habit, × ¼; s, flower, from above, × 4; t, opened corolla and staminal tube, × 4; u, stamen and anther, × 10; v, ovary with 3 sepals and bracteole, × 5; w, fruit, × 4; x, seed, × 20.

3. **Galax** L. Sp. Pl. 1: 200. 1753, partim, emend. Nutt. Gen. 1: 145. 1818, nom. cons.

Low herbs with scaly-bracted rhizomes forming a thick, matted tuft bearing long-petioled, round-cordate, crenate-toothed, lustrous evergreen leaves, the plant spreading by slender cord-like rhizomes which later become branched, thickened, and leaf-bearing at the tips. Flowers small (4–5 mm.), white, each with minute bracts at the base, borne in a wand-like raceme on a slender, naked scape in May (or July at higher altitudes). Sepals 1/3–1/2 the length of the oblong-spatulate petals. Petals distinct to the base, nearly erect or spreading. Filaments of 5 fertile stamens and 5 staminodia united, forming a tube adnate to the petals at the base, falling with the petals; free tips of the staminodia fleshy, nearly erect, the fertile anthers bent at right angles to the tube, connivent, each anther apparently 1-loculed and opening horizontally (actually across the top), the lower (inner) half tapering to an obtuse point. Pistil about as long as the calyx, the style short, the stigma 3-lobed. Capsule obpyriform, about 3 mm. long, without a columella, the seeds numerous, small, brown, angular, tapering, with a cellular seed coat. $2n = 12, 24$. (Not *Galax* L., 1754, nom. rejic.) TYPE AND SOLE SPECIES: *G. aphylla* L. (Name from Greek, *gala*, milk, presumably from the white flowers.) — GALAX, GALAXY, WAND-FLOWER, COLTSFOOT, BEETLEWEED, BEETLE-PLANT, SKUNK-CABBAGE.

A handsome and distinctive monotypic genus ranging from northern West Virginia and northwestern Maryland to the coastal plain of eastern Virginia and eastern North Carolina, to central Georgia, central Alabama and central Tennessee, in acid soils, generally in mesophytic associations with *Kalmia* or *Rhododendron* and other Ericaceae. The plant reaches its best development in rich, acid, humus-covered soils in the piedmont and Blue Ridge where, from North Carolina to Georgia, great quantities of the leaves, which become bronzed in winter, are gathered and sold to florists.

Galax provides one of the clearest, simplest and best studied cases of autoploidy in wild populations. Diploids occur throughout the range of the species, except in the Virginia coastal plain, where only the tetraploids are known. Tetraploid plants grow in the same habitats and areas as diploids, but are especially concentrated in the region from southern Virginia through the North Carolina mountains into South Carolina and Georgia. They appear to be absent from the northern and western parts of the range. Under the most favorable conditions the leaves of tetraploids may reach 15 cm. wide, while those of diploids attain only 10 cm. The plants are usually indistinguishable in the field, however, and no morphological distinctions other than those of size are known. No triploids and no meiotic irregularities have been reported in either diploids or tetraploids.

The apparently one-loculed anthers are strongly reminiscent of those of *Pyxidanthera* and suggest a similar mode of development. The flowers are most like those of *Pyxidanthera* (except for the presence of staminodia)

but in vegetative features *Galax* suggests *Shortia*. The genus has been treated either as the sole member of the tribe GALACINEAE or has been placed there with *Shortia* and *Berneuxia*.

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THE EFFECT OF JUVENILITY ON ROOTING OF CUTTINGS FROM APPLE SEEDLINGS

DONALD L. SMITH

IT HAS LONG BEEN KNOWN that cuttings from young seedlings can be rooted much more readily than can cuttings from mature trees. Extensive tests conducted by Gardner (1929) with seedlings of apple, pear, cherry, elm, locust, pine and spruce showed that cuttings from one-year-old seedlings rooted easily. He obtained some rooting from cuttings from two-year-old seedlings, but as the seedlings grew older it was difficult or impossible to root the cuttings taken from the upper branches.

It also has long been known that the basal part of the tree remains in the juvenile stage. More than 150 years ago Thomas Andrew Knight observed that shoots from the base of a seedling pear tree possessed juvenile characters and that scions from such shoots, when grafted on pear rootstocks, were much slower to come into fruit than scions from the bearing branches.

It is also known that cuttings taken from the lower branches of seedling trees will root more easily than cuttings taken from the tops of the mature trees (Grace, 1939; O'Rourke, 1951). The basal part of the tree appears to remain in the juvenile stage and a seedling tree can be kept in the juvenile stage indefinitely by cutting it back to the ground each year (Blair, 1955).

These observations on the relation of juvenility to ease of rooting of cuttings are of considerable significance in the clonal propagation of trees and shrubs. Clonal propagation of certain species by cuttings is essential to maintain a uniform root system. It is also essential in species such as the lilac, which suckers from the roots, if the clone is to be maintained true to type by the amateur horticulturist.

Seedling trees can be grown to maturity so that the flowers and fruits can be evaluated, but can still be propagated readily by cuttings by forcing sucker shoots from the base of the trunk. This can be done by girdling the bark near the base of the trunk or cutting the tree back nearly to the level of the ground. Less drastic methods are bark inversion or "scoring" the bark of the trunk near the base of the tree.

Tests were made on four-year-old seedlings of an ornamental apple, *Malus* 'Henry F. duPont,' grown in the Bussey Institution nursery during the summer of 1958. In June 1957 every other tree in the nursery row had a short ring of bark inverted to induce earlier flowering. The bark-inverted trees did not fruit earlier than the controls, but they did produce profuse suckering from the base of the tree. In some cases the sucker shoots bore leaves which were tri-lobed, even though the mature branches bore only entire leaves. In other cases there was little morphological difference be-

tween the juvenile and adult leaves. All of the trees tested fruited for the first time in 1958.

Cuttings from sucker shoots and from fruiting branches were taken in June. The cuttings, which were about eight inches long, were cut in half to provide basal and tip cuttings. Half of the cuttings were treated with Hormodin No. 2, while the other half were planted with no hormone treatment. The cuttings were set in wet sand in greenhouse flats, a wire frame was placed over them, and the entire flat and wire frame were enclosed in polyethylene film. The enclosed flats were set in the shade under the greenhouse bench and given no further attention until examined for rooting. The results are shown in TABLE I.

The juvenile cuttings of tree number 16155–4 rooted rather well with or without hormone treatment, but the adult cuttings rooted poorly or only moderately well, even with hormone, and very poorly, or not at all, without hormone. The juvenile cuttings of tree 16155–14 also rooted much better and earlier than did the adult cuttings. With tree 16155–21 the adult basal cuttings rooted comparatively well with hormone. In general the basal cut-

TABLE I. **Rooting of Cuttings from Juvenile and Mature Branches**

TREE NUMBER	TYPE OF CUTTINGS	HORMONE	NUMBER OF CUTTINGS	PER CENT ROOTED AFTER WEEKS 2	3	4	5	6
16155–4	J,T*	+	10	40		40	50	
"	J,T	−	10			40		50
"	J,B	+	10	80		90	90	
"	J,B	−	10			80		80
"	A,T	+	10	20		20	20	
"	A,T	−	10			0		0
"	A,B	+	10	0		50	50	
"	A,B	−	10			0		10
16155–14	J,T	+	8	75	87		100	
"	J,T	−	10			20		30
"	J,B	+	8	87	87		100	
"	J,B	−	10			100		100
"	A,T	+	8	0	0		0	
"	A,T	−	10			0		10
"	A,B	+	8	0	12		62	
"	A,B	−	10			20		40
16155–21	J,T	+	9	0	33		77	
"	J,B	+	9	11	77		77	
"	A,T	+	9	0	0		22	44
"	A,B	+	9	0	44		77	

* A = Adult; J = Juvenile; T = Terminal; B = Basal.

tings of either juvenile or adult branches rooted better than the terminal cuttings and the juvenile cuttings from the basal suckers rooted much better than the adult cuttings from fruiting branches. The cuttings which

rooted in two weeks were more likely to thrive when transplanted than those which required a longer time.

Cuttings from root suckers were also found to root more easily than cuttings from mature fruiting branches, even when the root suckers had developed six or seven feet from the base of the tree. Suckers from the roots were numerous on a *Malus sargentii* f. *rosea* hybrid (3340) which was 18 years old and growing in sod. Cuttings were made in the same manner as previously described. The results are shown in TABLE II. No rooting was obtained from the cuttings from the fruiting branches, but moderate rooting, with hormone, was produced in four weeks by cuttings from the root suckers. Evidently the roots retain their juvenility for a greater distance from the base of the tree than do the branches.

In the summer of 1957 Dr. Karl Sax found a seedling of Hopa Crab (*Malus baccata* × *pumila niedzwetzkyana*) which appeared to be promising as a dwarfing rootstock because of its thick bark — a characteristic of the extremely dwarfing rootstock varieties used in Europe. Cuttings from the original three-year-old seedling gave 91 per cent rooting in two weeks, and cuttings from lateral branches of the Hopa Crab seedling budded on *M. sargentii* f. *rosea* gave 100 per cent rooting in two weeks, using hormone (TABLE II). Even without hormone 85 per cent rooted in four weeks. These rooted cuttings were transplanted to soil, with no loss, for testing as a dwarfing rootstock and to see if they can be kept as permanent juveniles (as a source of cuttings) by keeping them cut back to the ground level each year.

TABLE II. **Rooting of Cuttings from Juvenile and Adult Seedlings**

TREE NUMBER	TYPE OF CUTTING	HORMONE	NUMBER OF CUTTINGS	PER CENT ROOTED AFTER WEEKS 2	3	4	5	6
33340	A.T.*	+	25	0		0		
"	A.T.	−	25	0		0		
"	R.T.	+	15	13		53		
Hopa Sdlg.	T	+	12	91				
"	S	+	12	100				
"	S	−	20	40		85		

* A.T. = Adult Terminal; R = Root sucker; T = Terminal; S = Secondary.

SUMMARY

Juvenile shoots from the base of fruiting seedling apple trees, induced by bark inversion, were found to root more readily than cuttings taken from the fruiting branches. Root suckers of a mature apple tree rooted well, although cuttings from the fruiting branches produced no roots, even with hormone treatment. A three-year-old seedling of Hopa Crab rooted very readily from cuttings to be tested as a dwarfing rootstock clone. The production and retention of juvenility in clonal varieties of trees and shrubs should be of value in clonal propagation.

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STUDIES IN THE GENUS COCCOLOBA, VII. A SYNOPSIS AND KEY TO THE SPECIES IN MEXICO AND CENTRAL AMERICA

RICHARD A. HOWARD

THE ONLY COMPLETE MONOGRAPH of the genus *Coccoloba* was prepared by Gustav Lindau and published in Engler's Botanische Jahrbücher **13**: 106–229. 1890. Since that time many additional species have been described in the genus as the result of extensive collecting by botanists in Mexico and in the several countries of Central America. Paul Standley revised *Coccoloba* as it occurs in Mexico in his treatment of the trees and shrubs of Mexico published in 1922. More recently Standley with Julian Steyermark treated the species of Guatemala as part of their series of papers on the flora of Guatemala. In addition, lists of species, some with critical notes, will be found in the following papers. Other papers and citations are included in the text.

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In general, the genus *Coccoloba* has been overdescribed in Mexico and Central America. Of the eighty names which have been applied in published form, only thirty-three species are recognized in this paper. In large part this tendency to excessive description is due to floristic treatments which deal individually with the many small countries of Central America. Many species which were considered endemic in adjacent countries have proved to be identical instead. Several West Indian species are now recognized in the Central American flora and the corresponding Central American name has been reduced to synonymy. Seven species had been described on the basis of sterile branches from adventitious shoots. All of these have now been associated with fertile material and these names placed

in synonymy. Fortunately only one such name had to be retained with a sterile holotype specimen. The failure to recognize the unisexual condition of the plants led to the duplication of specific names and several such species have now been properly associated. Two new species are described and one species has been removed from synonymy and re-established at the species rank.

Lindau in his monograph treated the species from Mexico and Central America in three sections of the genus. While these sections are useful in a preliminary assignment of species within the genus, the sections can not be maintained. When sufficient material is examined, intermediates are found and the sections grade indistinguishably into one another.

In the previously published studies [1] of the genus *Coccoloba* in the West Indies I had the advantage of extensive field work and an intimate knowledge of the variation found in the living plant. Much of the information gained in studying the West Indian species has been applied to the current study.

Many of the experienced field botanists who have described species of *Coccoloba* in Mexico and Central America have regarded the flowers as being perfect. The extensive group of herbarium specimens I have seen, as well as the living plants I have studied in Mexico and Honduras, clearly indicates, however, that the flowers are unisexual or functionally so. The pistillate flowers are normally borne singly at each nodule of the inflorescence rachis or rarely in clusters of two or three. The stamens of such flowers are rudimentary and included. The staminate flowers with pollen-producing, exserted stamens are borne in clusters of three or more.

Only a few species of Mexico and Central America have heavily coriaceous leaves or leaves much reduced in size. The leaves tend to be more pubescent than those of West Indian species. The variation in size between leaves of normal shoots and/or adventitious shoots is similar in the West Indies and in Central America. The leaves of adventitious shoots are larger, thinner and on longer petioles than those of normal shoots. Short-shoots, or at least shoots of limited growth, occurring laterally on the branches may also produce leaves smaller in size than those of shoots of normal growth. Pubescence varies with age of the leaf.

An adequate understanding of the species is best obtained from a study of staminate and pistillate flowers, fruits and leaves from both normal and adventitious shoots. I am grateful to the several collectors indicated in the text who made special efforts to get complete material for me. I have also been fortunate to be able to study nearly all the types of the species considered in this paper. I am particularly grateful to the directors and curators of the Botanisches Museum, Berlin; the Jardin Botanique de l'État, Brussels; the Royal Botanic Gardens, Kew; the Chicago Natural History Museum, Chicago; the Botanische Staatssammlung, Munich; and the University Herbarium, University of Michigan, Ann Arbor, for the significant materials sent for this study. Equally valuable but less authen-

[1] Jour. Arnold Arb. **30**: 388–424. 1949; **37**: 317–339. 1956; **38**: 81–106. 1957; **38**: 211–242. 1957; **39**: 1–48. 1958; **40**: 68–93. 1959.

tic specimens were received on loan from the other herbaria designated by the standard abbreviations given in Index Herbariorum.

Distribution of recognized species of Coccoloba in Mexico and Central America

	Greater Antilles	Mexico	Guatemala	Br. Honduras	El Salvador	Honduras	Nicaragua	Costa Rica	Panama	South America	Lesser Antilles
acapulcensis		×	×	×		×		×			
acuminata			×			×	×	×	×		
barbadensis		×	×		×						
belizensis			×	×		×	×				
caracasana		×	×		×		×	×	×		
chiapensis		×				×					
cozumelensis		×	×	×			×				
darienensis									×		
diversifolia	×	×	×								
goldmannii		×									
hondurensis		×	×	×		×					
humboldtii		×									
lasseri									×		
lehmannii								×	×	×	
liebmannii		×									
lindeniana		×									
lindaviana						×					
× *lundellii*				×							
manzanillensis									×		
matudai		×									
montana		×	×	×	×						
nicaraguensis							×				
novogranatensis			×						×	×	×
obovata								×	×	×	
padiformis								×	×	×	
parimensis									×	×	
reflexiflora		×	×	×		×					
spicata		×		×							
standleyana								×			
swartzii	×			×		×					×
tuerckheimii			×			×	×	×	×		
uvifera	×	×	×	×	×	×	×	×	×	×	×
venosa	×	×	×		×	×	×	×		×	×

The following list contains the names used for species of *Coccoloba* in Mexico and Central America. These names either were used in floras, lists or monographic treatments or apply to taxa based on specimens collected

in this area. The generic name *Coccoloba* has been conserved. *Coccolobis* is regarded as an orthographic variant and all binomials published under this spelling are also known as *Coccoloba*. The many transfers made by Otto Kuntze to the genus *Uvifera* have been omitted. All of the names in this list are discussed in the text under the recognized specific name. Varieties which are treated as distinct from the species are listed below. Varieties not listed are transferred with the species.

Campderia floribunda = **Coccoloba venosa**
C. lindeniana = **Coccoloba lindeniana**
C. mexicana = **Coccoloba venosa**
C. nematostachya = **Coccoloba manzanillensis**
Coccoloba acapulcensis Standley
C. acuminata HBK.
C. alagoensis major = **C. venosa**
C. allenii = **C. lehmannii**
C. anisophylla = **C. chiapensis**
C. barbadensis Jacquin
C. belizensis Standley
C. bracteolosa = **C. parimensis**
C. browniana = **C. acapulcensis**
C. cardiophylla = **C. acapulcensis**
C. caracasana Meisner
C. changuinolana = **C. lehmannii**
C. chiapensis Standley
C. colonensis = **C. reflexiflora**
C. coronata = **C. spicata**
C. corozalensis = **C. swartzii**
C. cozumelensis Hemsley
C. darienensis Howard
C. diversifolia Jacquin
C. emarginata = **Neomillspaughia emarginata** (Gross) Blake
C. escuintlensis = **C. montana**
C. excelsa glabra = **C. parimensis**
C. excoriata = **C. venosa**
C. floribunda = **C. venosa**
C. fluviatilis = **C. barbadensis**
C. gentlei = **C. swartzii**
C. goldmannii Standley
C. grandifolia Standley = **C. liebmannii**
C. guatemalensis = **C. tuerckheimii**
C. hirsuta = **C. belizensis**
C. hondurensis Lundell
C. humboldtii Meisner
C. jurgenseni = **C. barbadensis**
C. lancifolia = **C. diversifolia**
C. lapathifolia = **C. liebmannii**
C. laurifolia = **C. diversifolia**
Coccoloba lasseri Lundell
C. latifolia = **C. tuerckheimii**
C. lehmannii Lindau
C. leptostachya = **C. barbadensis**
C. liebmanni = **C. liebmannii**
C. liebmannii Lindau
C. lindaviana Howard
C. lindeniana (Bentham) Lindau
C. lundellii = **C. × lundellii**
C. × lundellii Standley
C. macrophylla = **C. rugosa** Desfontaines
C. manzanillensis Beurling
C. manzinellensis = **C. manzanillensis**
C. marginata = **C. hondurensis**
C. masoni = **C. barbadensis**
C. matudai Lundell
C. mayana = **C. barbadensis**
C. molinae = **C. venosa**
C. montana Standley
C. nematostachya = **C. manzanillensis**
C. nicaraguensis Standley & L. Williams
C. nivea = **C. venosa**
C. novogranatensis Lindau
C. oaxacensis = **C. barbadensis**
C. obovata HBK.
C. orizabae = **C. humboldtii**
C. padiformis Meisner
C. parimensis Bentham
C. petrophila = **C. humboldtii**
C. pubescens = **C. liebmannii**
C. roseiflora = **C. padiformis**
C. reflexiflora Standley
C. riparia = **C. obovata**
C. sessiliflora = **C. barbadensis**
C. schiedeana = **C. barbadensis**
C. schippii = **C. montana**
C. spicata Lundell
C. steyermarkii = **C. montana**
C. standleyana Allen
C. strobilulifera = **C. acuminata**
C. suborbicularis = *C. × lundellii*
C. swartzii Meisner

Coccoloba tuerckheimii Donnell Smith
C. umbilicata = **C. pyrifolia** Desfontaines
C. uvifera Linnaeus
C. venosa Linnaeus
Coccoloba *waittii* = **C. novogranatensis**
C. wercklei = **C. acapulcensis**
C. yucatana = **C. cozumelensis**
Uvifera lehmanni = **Coccoloba lehmannii**

The following is a synoptic key to the species of Mexico and Central America. To be fully applicable, the key requires both flowers and fruit. It does not apply to sterile material, particularly that of adventitious shoots.

Following the key, the species are listed in alphabetical order with a citation of specimens seen and a discussion of the nomenclature adopted. The countries are considered in order from north to south, with the states, provinces, districts, etc., in each country being listed alphabetically.

KEY TO THE SPECIES

1. Petioles arising from above the base of the ocrea, the diameter of the leaf scar smaller than the distance from the base of the leaf scar to the base of the ocrea.
   (Species inadequately known: Leaves lanceolate-ovate, deciduous, the young leaves turning black on drying. ..... *C. nicaraguensis.*)
   2. Inflorescence paniculate.
      3. Inflorescence branches few; leaf base rounded or cordate; fruit spherical, rounded at the base. ..... *C. lasseri.*
      3. Inflorescence many-branched; leaf blade acute at the apex, the base decurrent on the petiole; fruit oval, stalked at the base. ..... *C. tuerckheimii.*
   2. Inflorescence racemose or spicate.
      4. Inflorescence racemose.
         5. Leaves narrowly oblong to narrowly elliptic. ..... *C. lindaviana.*
         5. Leaves cordate, elliptic or obovate-elliptic.
            6. Leaves cordate, the base strongly cordate, occasionally peltate; flowering and fruiting pedicels 5–15 mm. long; fruit globose, 1 cm. diameter, or abnormally obovoid and 2.5 cm. long; ocreae splitting longitudinally, flaring, the petiole appearing winged at the base; the inflorescence ocrea often appearing spathe-like. ..... *C. acapulcensis.*
            6. Leaves elliptic to obovate-elliptic, flowering and fruiting pedicels shorter; ocrea not flaring if split.
               7. Leaves usually narrowed to a cordate-auriculate base; ocreolae conspicuous, papery, flaring; flowers never reflexed; fruit globose, conspicuously coronate. .. *C. novogranatensis.*
               7. Leaves rounded at the base or narrowed to an obtuse base; ocreolae small and inconspicuous, the flowers commonly reflexed; fruit narrowed at the base and obtuse, at most slightly coronate, at the apex. ..... *C. reflexiflora.*
      4. Inflorescence spicate, the fruits essentially sessile.
         8. Leaves tan-colored when dry, the petioles usually grayish green; leaf blades acute to obtuse at the apex; fruit globose, obtuse at the apex. ..... *C. spicata.*

8. Leaves and petioles turning dark brown or black on drying; leaf blades acuminate at the apex; fruit elongate, the achene stoutly coronate at the apex. ..... *C. obovata.*

1. Petioles arising from the base of the ocrea, the base of the leaf scar at or close to the base of the ocrea.
(Species inadequately known: ..... *C. standleyana.*)
9. Inflorescence paniculate.
10. Flowering pedicels stout, not exceeding the ocreolae; young stems, ocreae and inflorescence rachis conspicuously puberulent or tomentose to pilose on adventitious shoots, the pubescence golden or chestnut-colored; the terminal buds large, conspicuously club-shaped, swollen and rounded at the apex, the ocrea of the terminal bud commonly subcalyptrate; fruit globose, not narrowed to a stalk at the base, obtuse or rounded, not coronate, at the apex. .... *C. belizensis.*
10. Flowering pedicels tenuous, exceeding or up to twice the length of the ocreolae; young stems, ocreae and inflorescence rachis puberulent, the pubescence commonly noticeable only with a lens; the terminal bud slender, acute at the apex, the ocrea splitting laterally; mature fruits not known. ..... *C. matudai.*
9. Inflorescence racemose or spicate.
11. Inflorescence racemose; the flowers and fruits borne on pedicels which exceed the bracts and the ocreolae.
12. Lianas; leaf blade umbonate between the veins. . . *C. parimensis.*
12. Trees or shrubs, at most the ends of the branches rarely scrambling.
13. Leaves as broad as or broader than long, orbicular to broadly oblong, apex rounded to emarginate.
14. Fruits 1–2.5 cm. long, obtuse or rounded at the apex, at most very slightly coronate, usually slightly stalked at the base.
15. Leaves usually much broader than long, the base strongly cordate with one lobe of the blade usually slightly overlapping the petiole. ..... *C. uvifera.*
15. Leaves usually orbicular, the base of the blade essentially rounded or obtuse. .... *C.* × *lundellii.*
14. Fruits less than 1 cm. long.
16. Fruit strongly coronate at the apex, the base rounded; leaf blades persistently pubescent only along the midrib and primary veins or glabrate.
..... *C. barbadensis* hybrid.
16. Fruit elongate, the perianth lobes distinct on the upper 1/3 or 1/2 of the fruit; leaf blades persistently pubescent on the lower surface.
..... *C. goldmannii.*
13. Leaves noticeably longer than broad.
17. Leaves elliptic-lanceolate in outline, acuminate to long-acuminate at the apex, cuneate or rounded to an obtuse asymmetrical base; petioles 2–6 mm. long.
..... *C. chiapensis.*
17. Leaves not of this type.
18. Foliar ocreae 3–5 cm. long, membranaceous or

chartaceous, silky pubescent, fruit coronate at the apex, the crown surrounded by the distinct perianth lobes, these fused below. ..... *C. manzanillensis.*

18. Foliar ocreae 1–2 cm. long, coriaceous, or if chartaceous, not silky pubescent.
    19. Achene surrounded by the expanded perianth lobes, these free nearly to the base.
        20. Leaves elliptic to elliptic-oblong. the flower clusters distinct on the inflorescence rachis. ..... *C. lehmannii.*
        20. Leaves narrowly oblong or obovate-oblong, the inflorescence of closely associated flower clusters and these not clearly distinct on the rachis and not appearing interrupted.
            21. Leaves obovate-oblong. broadest above the middle; midrib and veins usually pubescent below, blades persistently barbate in the axils of the primary veins. ..... *C. venosa.*
            21. Leaves narrowly oblong, broadest at middle; leaves glabrous below. ..... *C. darienensis.*
    19. Achene surrounded by the expanded hypanthium, the perianth lobes coronate or surrounding the upper third of the achene.
        22. Fruit conspicuously coronate.
            23. Leaves lanceolate-ovate in outline, ocreae glabrous; pedicels in fruit several times as long as the thickness of the inflorescence rachis. ..... *C. diversifolia.*
            23. Leaves broader, ovate-oblong to obovate-elliptic in outline, ocreae puberulent; fruiting pedicels not longer than the thickness of the inflorescence rachis.
                24. Fruiting pedicels shorter than the ocreolae; leaves usually rounded or with a short, bluntly acute apex, concolorous. ..... *C. barbadensis.*
                24. Fruiting pedicels slightly longer than the ocreolae; leaves usually with a short but sharply acuminate apex, dark or black on the upper surface and lighter below. ..... *C. hondurensis.*
        22. Fruit obtuse at the apex, the perianth lobes imbricate over the obtuse apex of the achene.

25. Leaves persistently pubescent below, the margin entire but usually conspicuously crispate to undulate. ..... *C. liebmannii.*

25. Leaves glabrous, the ocreae or petioles puberulent or glabrous, margin of the blade entire or flat or slightly recurved but not crispate-undulate.

26. Ocreolae conspicuous in flower and fruit, membranaceous and flaring; fruit as broad as or broader than long, rounded to slightly stalked at the base, slightly acute at the apex. ..... *C. montana.*

26. Ocreolae small and inconspicuous, appressed and not flaring; fruit longer than broad, rounded or obtuse at the apex and the base.

27. Upper leaf surface with the ultimate venation conspicuously reticulate when dry, the ocreae and petioles puberulent. .. *C. humboldtii.*

27. Upper leaf surface plain between the primary veins, the ultimate venation not evident; ocreae and petioles glabrous. ..... *C. padiformis.*

11. Inflorescence spicate, the pedicels shorter than the bracts and ocreolae in flower and fruit or, if protruding beyond the ocreolae, the visible portion less than the diameter of the inflorescence axis.

28. Inflorescence rachis swollen at the flower clusters and tapering below them, the flowers appearing at an acute angle to the axis; the lobes of the perianth expanded in fruit and covering at least the upper half of the achene. ..... *C. acuminata.*

28. Inflorescence rachis of uniform thickness and not expanded to each flower cluster, the flowers borne flat or at right angles to the axis.

29. Ocreolae conspicuous in flower and fruit, membranaceous or chartaceous.

30. Leaves narrowly oblong, acute to acuminate at the apex; fruit not known. ..... *C. lindeniana.*

30. Leaves broadly oblong to orbicular, often broader than long, the apex rounded or emarginate; the lobes of the perianth expanded in fruit and covering more than half of the achene. ..... *C. caracasana.*

29. Ocreolae small, not conspicuous in flower or fruit; the

hypanthium surrounding the achene in fruit, the perianth lobes imbricate or coronate.

31. Leaves narrowly ovate to ovate-lanceolate, generally cordate at the base, rarely rounded or obtuse, acuminate at the apex, generally drying to a pale tan color, the petioles usually grayish when dry, the petioles and ocreolae puberulent but rarely tomentose; the blades 3–9 cm. long. ..... *C. cozumelensis.*

31. Leaves rounded or obtuse at the base, acute or obtuse at the apex, the blades turning dark on drying, the petiole almost black when dry; glabrous (in Central America).

32. Leaves of fertile branches generally with blades 12–20 cm. long and 8–12 cm. broad; inflorescences densely flowered; fruit obtuse at the apex and only slightly coronate. ..... *C. hondurensis.*

32. Leaves of fertile branches usually with blades 7–11 cm. long and 5–6.5 cm. broad; inflorescence axis sparsely flowered, the flower clusters distinct and separated; fruit rounded at the apex and distinctly coronate. ..... *C. swartzii.*

Coccoloba acapulcensis Standley, Proc. Biol. Soc. Wash. **33**: 66–67. 1920.

Coccoloba cardiophylla Standley, Publ. Field Mus. Bot. **8**: 8. 1930.
Coccoloba browniana Standley, Trop. Woods **10**: 4. 1927.
Coccoloba wercklei Standley, Publ. Field Mus. Bot. **4**: 304. 1929.

It is unfortunate that the oldest name applicable to this species is based on anomalous material. To the present, *Coccoloba acapulcensis* has been distinguished by the peltate leaves and the large fruits. The collections cited below, made since the type collection of the species, show clearly that leaves with peltate, cordate or rounded bases may be found on the same shoot. Miranda (Anal. Inst. Biol. México **14**: 29. 1943) reports that peltate leaves appear abundantly on all young specimens of *C. acapulcensis* but that the cordate base is more frequent on older plants. The fruits of this species are larger than is usual in the genus *Coccoloba*; however, the fruits of the holotype appear to be abnormal, the probable result of an insect attack. Similar abnormal pedicels also occur on the type specimens of the other species which I have examined and which I now consider to be synonymous with *C. acapulcensis*.

Lundell (Lloydia **2**: 83. 1939) placed *Coccoloba cardiophylla* in the synonymy of *C. browniana* and reported the affinities of the species to be with *C. wercklei*, of Costa Rica, and *C. acapulcensis*, of Guerrero, Mexico. In the original description of *C. wercklei* Standley suggested that his new species is a relative of the Honduran *C. browniana* but distinct from it in that *C. browniana* bears pedicels only 5 mm. long. The series of specimens cited, however, shows the full range of variation in the length of the pedicel between flowering and mature fruiting conditions, as well as the differences

in the pedicel length of the male and female flowers. It is clear to me that all four species must be grouped together under the oldest accepted name, which is *C. acapulcensis*.

México. GUERRERO: Acapulco, *MacDaniels 249* (F), *Haenke 1120* (F), *1125* (F), *Palmer 399* (US-type of *C. acapulcensis*; GH, NY); Tecpán de Galiana, *Hinton 14118* (F, GH). YUCATÁN: Chichén Itzá, *Bequaert 28* (A, F), *C. L. & A. A. Lundell 7471* (DS, F, MICH), *7513* (A, DS, F, MICH); Kancabdzonot, *Gaumer & sons 23865* (DS, F, GH), *23905* (F); Quintana Roo, *C. L. & A. A. Lundell 7644* (MICH); Ebtún, *C. L. & A. A. Lundell 7534* (A, DS, F, MICH); without specific location, *Gaumer 24013* (F-type of *C. cardiophylla;* A, GH). **Guatemala.** EL PROGRESSO: Barranquilla, *Steyermark 46428* (F). HUEHUETENANGO: Between Democracia and canyon of Chamusú, *Steyermark 51229* (F); Paso del Boquerón, *Steyermark 51152* (F). JUTIAPA: Quebrada above Ovejero, *Standley 77647* (F). **British Honduras.** ORANGE WALK DISTRICT: Honey Camp, *Lundell 514* (A, DS, F, GH). **Honduras.** COMAYAGUA: Comayagua, *Standley & Chacón 5126* (F), *5383* (F), *5484* (F), *6012* (F); El Banco, *Rodriguez 2374* (F, GH); Río Selguapa, *Rodriguez 2616* (F, GH); Siguatepeque, *Yuncker, Dawson & Youse 6138* (F, GH, MICH). YORO: Coyoles, *Yuncker, Koepper & Wagner 8071* (F, GH, MICH); Olanchito, *Record & Kuylen H–54* (US-type of *C. browniana;* GH, Y). **Costa Rica.** El Coyolar, *Wercklé s.n.* (US 865109-type of *C. wercklei*); San Pedro de San Ramón, *Brenes 21872* (F).

Coccoloba acuminata HBK. Nov. Gen. 2: 176. 1817.

Coccoloba acuminata var. *pubescens* Lindau, Bot. Jahrb. 13: 193. 1890.
Coccoloba acuminata var. *glabra* Lindau, l.c. 194.
Coccoloba strobilulifera Meisner, Fl. Bras. 5(1): 25. 1855.

Lindau was correct in concluding that *Coccoloba strobilulifera* Meisner is the same as *C. acuminata*. I have examined the specimens cited by Meisner and Lindau and have also seen this species in the field. On the basis of these observations, I find it impossible to recognize the two varieties that Lindau established on a characteristic of the pubescence. The variation in the amount of pubescence seems to be related to the age and vigor of the plant. Pubescence is present on the young leaves and shoots but is less conspicuous, or the hairs are broken off so that only the clear hair bases remain, on older specimens. Certainly all intermediate stages can be found between the material cited by Lindau as *C. acuminata* var. *pubescens* and that cited as var. *glabra*.

In addition to the material cited below, I have seen collections from Colombia, Venezuela, British Guiana, Brazil, Ecuador and Peru. The type is *Humboldt 1479*, collected along the Río Magdalena, near Mompox, Colombia. Lindau did not select a type for his var. *glabra*, but the type of *C. strobilulifera* Meisner is *Moritz*, without number and without definite locality in Colombia. Lindau places this species in synonymy under his var. *glabra*.

Guatemala. IZABAL: Quebradas, *Pittier 8592* (GH); between Bananera and Sioux Station, *Steyermark 38986* (F, MICH). **Honduras.** ATLÁNTIDA: Near Tela, *Mitchell 82* (F, GH); near Tela, *Standley 54710* (A, F); La Fragua, *Standley*

55720 (F); vicinity of Tela, *Standley 56867* (F); vicinity of San Alejo, *Standley 7771* (F); between Tela and Lancetilla, *Yuncker 4645* (A, F, GH, MICH). CORTÉS: La Lima, *Johansen 45* (A, F); Río Piedras near San Pedro Sula, *Molino 3417* (F); La Lima, *Standley & Chacón 7556* (F), *Williams & Molina 12485* (F). YORO: Near Progresso, *W. D. Hottle 1* (F), *Record & Kuylen H–44* (GH), *Standley 55013* (A, F); Coyoles, *Yuncker, Koepper & Wagner 8034* (F, MICH), *8061* (F, GH, MICH). Department unspecified: Coyol, *Carleton 495* (A, GH); Highland Creek, Pto. Sierra, *Wilson 84* (F). **Nicaragua.** ZELAYA: La Esperanza, Río Grande, *Molina 2109* (F), *2136* (F, GH). Department unspecified: Region of Braggman's Bluff, *Englesing 183* (F, Y), *229* (F, Y). **Costa Rica.** ALAJUELA: Vicinity of Capulín, Río Grande de Tárcoles, *Standley 40189* (F). PUNTARENAS: Canton de Osa, Palmar Norte to Cañablancal, *Allen 5226* (GH, MICH). **Panamá.** CANAL ZONE: Barro Colorado Island, *Aviles 74, 976* (F), *L.H. & E.Z. Bailey 616* (GH), *Bangham 378* (A, F), *Starry 223* (F), *Wilson 22, 140* (F), *Woodworth & Vestal 397* (A, F); Juan Mina, Chagres River, *Bartlett & Lasser 16321* (MICH); Gamboa Reach, *Maggs II 39* (F); Frijoles, *Maxon 4707* (F, GH); Gamboa, *Pittier 2608* (F, GH, MO); Upper Chilibre River, *Seibert 1510* (MO); Quebrada Bonita, *Steyermark & Allen 17194* (MICH, MO). DARIEN: Tucuti, Chepigana, *M. E. & R. A. Terry 1381* (A, F, MO); Yape, *Allen 850* (F, GH, MO); location unspecified, *MacBride 2676* (F). Province unspecified: Maume & Gorgone, *Wagner s.n.* (M); Marraganti, *Williams s.n.* (NY). Location unspecified: *Weddell s.n.* (GH, P).

Coccoloba barbadensis Jacquin, Enum. 36. 1760, Obs. Bot. 1: 18. *pl. 8.* 1764; Howard, Jour. Arnold Arb. 37: 317–339. 1956.

Coccoloba barbadensis var. *mexicana* Meisner, DC. Prodr. **14**: 153. 1856.
Coccoloba schiedeana Lindau, Bot. Jahrb. **13**: 187. 1890.
Coccoloba jurgenseni Lindau, Bot. Jahrb. **13**: 188. 1890.
Coccoloba leptostachya Bentham, Bot. Sulph. 159. 1856.
Coccoloba oaxacensis Gross, Repert. Sp. Nov. **12**: 219. 1913.
Coccoloba mayana Lundell, Bull. Torrey Club **64**: 547. 1937.
Coccoloba masoni Lundell, Lloydia **2**: 8. 1939.
Coccoloba fluviatilis Lundell, Contr. Univ. Mich. Herb. **7**: 8. 1942.

In the second paper of this series (Jour. Arnold Arb. 37: 317–339. 1956), I considered the correct identification and application of the names *Coccoloba swartzii* Meisner and *C. barbadensis* Jacq. The former name had been overlooked by recent workers on the floras of the Antillean Islands and the latter name had been misapplied. I concluded that the material which is properly called *C. swartzii* was first identified by Lindau as *C. barbadensis* and that later he and all recent authors on the West Indian flora used the name *C. diversifolia* Jacq. for the same material.

Coccoloba barbadensis Jacq. was described twice by Jacquin, first in his Enumeratio, and later, supported by an illustration, in his Observationum Botanicarum. A definite location was not given for the species and recent authors have assumed from the name that the island of Barbados was implied. However, in the British Museum (Natural History) there are two sheets which can be referred to the Jacquin description and illustration and these are significant in the correct application of the name. One of

these, from the Miller herbarium, is obviously the material illustrated by Jacquin. Moreover, it bears the Houston catalogue reference which Jacquin cites in the synonymy of his *Coccoloba barbadensis*. Houston collected in Campeche (Yucatán) and his specimen is accurately matched in many of the collections cited below.

In his monograph of the genus *Coccoloba* for De Candolle's Prodromus, Meisner assumed that *C. barbadensis* came from the West Indies and so created a variety, *C. barbadensis* var. *mexicana*, for a Schiede specimen from Mexico. Lindau (Bot. Jahrb. 13: 187. 1890) recognized the variety as a species which he named *Coccoloba schiedeana*, citing in synonymy *C. barbadensis* var. *mexicana* Meisner. Lindau cited additional material, all of which, with the exception of one collection, I have now seen. These are all clearly comparable to the original Jacquin material; thus, *C. barbadensis* Jacq. must henceforth be considered in the flora of Mexico and Central America.

Of the two old specimens in the British Museum (Natural History), one represents a sterile adventitious shoot and the other a vigorous shoot with an old inflorescence from which the fruits have fallen. In all probability, therefore, it will be impossible to describe the fruit which accompanied this original sheet. However, with a knowledge of the variation found in other species of *Coccoloba* in such characteristics as leaf shape, size of petiole, presence or absence of pubescence and length of fruiting pedicels, it is possible to make an accurate comparison with more recent collections. It is clear that *C. barbadensis* has puberulent to tomentose ocreae and inflorescence rachises, although in age these become glabrous. Also, the leaves are coriaceous and the leaf shape, particularly at the base, is variable. As in other species of *Coccoloba*, the plants are dioecious and the pistillate flowers, and later the fruits, are borne on short pedicels which in length barely exceed the ocreolae. The fruit, coronate at the apex, is rounded at the base and not attenuated into a stipe.

The variations with age and environment in these characteristics have caused *Coccoloba barbadensis* to be described many times. Seven species are assigned to the synonymy of *C. barbadensis* in this paper alone. Three additional apparently unpublished names have been applied to the specimens in various herbaria. The original variety which Meisner described is also placed in synonymy with the species. Three of these newly recognized synonyms represent only sexual variations, i.e., staminate versus pistillate plants, in the comparisons given by the original authors. Two species were originally distinguished through the failure of the author to recognize the loss of, or to see the residual, pubescence. One species was based on an abnormal fascination of the inflorescence and two others were based on size and texture differences of the leaves. When considered alone or with only the material cited by the original authors, several of the species which I have reduced to synonymy might well represent clones or local populations. When considered with the wealth of material cited below, the differences become of little taxonomic value. It appears desirable to treat *Coccoloba barbadensis* as a widespread species of central and southern Mexico

and northern Central America, recognizing the considerable variation in leaf size, shape and texture.

Two excellent series of collections by Dr. Robert Dressler made in the states of Veracruz and Guerrero, Mexico, show the variation in leaf-size, -shape and -pubescence to be found on single plants.

Coccoloba leptostachya Bentham has been a troublesome name. Bentham described this plant, without citing a collection, in reporting on the Botany of the Sulphur Expedition. The locality was given as Libertad in Colombia, and recent collections from Colombia and Panama have been assigned to this species. However, examination of the type material in the Herbarium at the Royal Botanical Gardens at Kew shows clearly that the specimen on which Bentham based the species is a Barclay collection which represents *C. barbadensis*. Other species from the Sulphur voyage reportedly collected in "Libertad in Colombia" have more recently been recognized as Central American and, in several instances, the collection is believed to have come from Libertad in El Salvador. *Coccoloba leptostachya* appears to me to be a similar example of the incorrect citation of a locality. The recent collection *Carlson 563* (F) from "Finca Santa Emilia west of La Libertad at or near sea level" in El Salvador is a perfect match for the Barclay specimen. No material comparable to the type of *C. leptostachya* has been seen from Colombia.

In his monograph Lindau distinguishes *Coccoloba jurgenseni* from *C. schiedeana* on the basis of a glabrous inflorescence rachis in the former and a pubescent one in the latter. The distinction is inadequate, especially since the holotype of *C. jurgenseni*, *Jurgensen 157* (G) shows a slight puberulence within the range of variation expected in this genus.

Coccoloba oaxacensis Gross was reduced to the synynomy of *C. schiedeana* by Standley in his treatment of the trees and shrubs of Mexico. He reported at the time that he had "seen no material of *C. oaxacensis*, and it may be a distinct species." I have examined the holotype in the Berlin herbarium but find no reason to maintain *C. oaxacensis* as a species.

Coccoloba mayana Lundell was based on a staminate flowering specimen collected by Lundell on the bank of the Río San Pedro de Martir above El Paso in the Department of Petén, Guatemala. Lundell reported that the species was found only in wet soils on river banks and around "aguadas." *Coccoloba mayana*, he states, "is related to *Coccoloba schiedeana* Lindau, from which it differs in having longer racemes, nodes 1- or 2-flowered, larger flowers, and suborbicular perianth lobes." None of these characteristics is of specific value. At best, *C. mayana* as conceived by Lundell is an ecological variation, distinct only in having smaller and thinner leaves, but it does not seem to be worth a subspecific category. *Coccoloba barbadensis* is a variable species and, judging from the collections seen, occurs primarily in drier areas. Plants from other departments in Guatemala show larger leaves of thinner texture and are thus intermediate between the type collection of *C. mayana* and *C. barbadensis*.

Coccoloba masoni Lundell was based on a collection by H. L. Mason from Maria Magdalena Island of the Tres Marias Islands off the coast of

Nayarit, Mexico. Lundell recognized the dioecious condition of the flowers, the obovate or oval leaf shape and the pilose pubescence in the axils and on the veins of the leaves as distinguishing characteristics of this species. Two other collections from the same island group, one made earlier and one made later than the Mason specimen, show more clearly the range of variation in leaf-shape and -pubescence and indicate that *C. masoni* and the Mason collection on which it is based are the same as *C. barbadensis*. Only a few recent floras have recognized the dioecious nature of *Coccoloba*. At present it appears that all species are functionally unisexual and the dioecious character is not of specific value in the case of *C. masoni*.

In describing *Coccoloba fluviatilis*, Lundell placed his new species in a group which included *C. jurgenseni* and *C. mayana*, both of which are here included in *C. barbadensis*. Lundell felt that *C. fluviatilis* was distinct because of "large glabrous leaves, subcordate at the base, the stout petioles up to 1.7 cm. long, the glabrous rachis of the inflorescences, and the subsessile fruits." However, all of the size and shape characteristics mentioned by Lundell can be found in many of the single collections cited. The "glabrous" characteristic, however, is an error, for pubescence can be found on the terminal buds and in the axils of the leaves on the holotype, although the plants do become glabrate in the clonal material which Lundell studied.

Seler 1642 from Arroyo de San Carlos, in Mexico, was designated by Gross as the type of an apparently unpublished species named for the large, fasciated inflorescence axis. Many of Gross' new species have been published in obscure papers, so it is possible that this name may be in print. The fasciated inflorescence rachis is relatively common in other species of the genus and has been seen in three additional collections cited below. The Seler collection is clearly identical with the material assigned to this species.

The collection by Edward Palmer which was distributed with the letter "G" in place of a collector's number bears an unpublished name attributed to Rose. This name refers to the sessile flowers, but the collection is not distinct from *C. barbadensis*.

The specimen attributed to Galeotti and numbered *7218* has been cited and annotated by Lindau as *C. schiedeana*. The material, however, is a mixed collection containing in part *C. barbadensis* and *C. venosa*.

México. CAMPECHE: Champotón, *Flores 1934* (F); Mundo Nuevo, *Karwinsky 733b* (LE). CHIAPAS: Escuintla, *Matuda 2028* (A, DS, F, MICH); Javalinero, Palenque, *Matuda 3634* (A, F, MICH); Malpaso, near Siltepec, *Matuda 4517* (MICH-type of *C. fluviatilis*; A, F); Chicomuselo, *Matuda 15627* (F); Montecristo, *Matuda 15948* (F); Nandolopez, Acapetahua, *Matuda 16642* (BR, F); Mojarra, Tonalá, *Matuda 17139* (F); Mapastepec, *Matuda 17517* (F); Monserrate, *Purpus 275* (LE, US). COLIMA: Paso del Río, *Emrick 168* (F); Manzanillo, *Ferris 6209* (DS), *Palmer "G"* (B, GH, NY); Colima, *Palmer 90* (A, C, MICH). GUERRERO: La Mina near Atoyac, *Dressler 1798a, 1798b, 1798c* (GH); Vallecitos, Montes de Oca, *Hinton 10209* (DS, MICH), *10221* (DS, LE, MICH); Vallecitos, Llano de Oca, *Hinton 11781* (DS, LE, MICH); Sierrita, El Limón,

Galeana, *Hinton 14137* (F, GH); Chilpancingo, *Kenoyer C–277* (MICH); La Copradilla, *Langlassé 134* (B, GH); El Trienta, *C.L. & A.A. Lundell 12588* (MICH); Dos Arroyos, *Nelson 7029* (GH, NY); Acapulco, *Palmer 344* (A, GH), *602* (A, F, GH, MICH). JALISCO: Navidad, *McVaugh 11903* (MICH); Tuxpan, *Mexia 1051* (A, F, GH). MICHOACÁN: San Naranjillo, Coalcomán, *Hinton 13943* (GH); La Placita, *Turner 2028* (MICH). NAYARIT: Acaponeta, *Rose 1414* (NY), *Rose, Standley & Russell 14399* (NY); Magdalena Island, Tres Marias Islands, *Elmore 1B3* (F, MICH), *Nelson 4315* (GH), *Mason 1806* (F-holotype of *C. masoni*; A, DS, GH, MICH), *Maltby 167* (NY); San Blas, *Ferris 5331* (A, DS); Ixtlán, *Viereck 1193* (US). OAXACA: Rincón San Antonio, *Endlich* (B-holotype of *C. oaxacensis*); Dunes del'Oc. Pacifique, *Galeotti 7218*, in part (BR, K, P); Pinotepa Nacional, *Jurgensen 157* (G-type *C. jurgenseni*; F-photo & fragment; B, K); Between Llano Grande and Pinotepa, *Nelson 2334* (GH); Puerto Angel, *Reiche 574* (M); Arroyo de San Carlos, *Seler 1642* (B, GH); Almoloya, *L. Williams 9906* (F, W). SINALOA: Labradas, *Ferris & Mexia 5291* (A, DS). VERACRUZ: Laguna Encantada, east of San Andrés Tuxtla, *Dressler 1804a, 1804b, 1804c* (GH), *Nelson 452* (A); Tantoyuca, *Ervendberg 364* (GH, K, P); Savana de Mata de Don Juan, *Karwinsky 734, 735* (LE); Tajín, Papantla. *Kelley 65a* (GH); Laguna Tamiahua, south of Tampico, *LeSueur 100* (F); location unspecified, *Liebmann s.n.* (B); Mirador, *Ross 802* (M); Tierra Blanca. *Ross 883* (M); Zacualpan, *Purpus 12022* (F, MICH); Rancho Camarón, *Purpus 13068* (A, F, GH, MICH); Fortin, near Zacualpan, *Purpus 2428* (A, F, GH); Papantla, *Schiede s.n.* (LE-type of *C. barbadensis* var. *mexicana* and *C. schiedeana* by implication; B). State unspecified: location unspecified, *Houston s.n.* (BM-type of *C. barbadensis*); *Sessé & Mociño 950, 5434* (F).

Guatemala. ESCUINTLA: Naranjo, *J. Donnell Smith 2496* (F, GH); San José, *Standley 63998* (F); Río Guacalate, northwest of Escuintla, *Standley 89345, 89350* (F, MICH); Río Michatoya, southeast of Escuintla, *Standley 89054, 89060* (F, MICH). HUEHUETENANGO: Ciénaga de Lagartero below Miramar, *Steyermark 51488* (A, F). PETÉN: La Libertad, *Aquilar 275* (F, MICH, W), *313* (A, MICH), *Lundell 3230* (F, GH, MICH), *3212, 3340* (F, MICH); El Paso, *Lundell 1498* (MICH-holotype of *C. mayana*; DS, GH). QUEZALTENANGO: Río Ocosito, *J. Donnell Smith 1481* (F, GH). RETALHULEU: Champerico, *Standley 66593, 66602, 66631* (F); between Nueva Linda and Champerico, *Standley 87699, 87721* (F); Retalhuleu.*Standley 88818* (F). SAN MARCOS: Ocós, *Steyermark 37780* (F). SANTA ROSA: Guazacapán, *Standley 78603* (F); Chiquimulilla, *Standley 78785, 79175, 79243* (F); La Sepultura, west of Chiquimulilla, *Standley 79378* (F). SUCHITEPÉQUEZ: South of Tiquisate, *Steyermark 47807* (F).

Salvador. AHUACHAPÁN: Ahuachapán, *Standley & Padilla 2615* (F). *Standley 20313* (GH, MICH). LA LIBERTAD: Libertad, *Barclay s.n.* (K-type of *C. leptostachya*), *Carlson 563* (F). SANTA ANA: Santa Ana, *Standley 20404* (GH). SONSONATE: Acajutla, *Standley 21895, 21974* (GH).

The following collections are also assigned to *Coccoloba barbadensis*, but probably represent a hybrid complex. The specimens are all staminate, with sterile, insect-infested fruits on tenuous pedicels twice as long as the ocreolae. The leaves appear to be more coriaceous and the margins are revolute. The leaves are shiny on the upper surface, although this may be an artifact of preservation.

Guatemala. ALTA VERAPAZ: Laguna Sapalá, *Steyermark 44899* (F). PETÉN:

Laguna Petexbatúm, *Steyermark 46224* (A, F); Along Río Santa Mónica between Cedral and Ceibal, *Steyermark 46040* (F, MICH), *46160* (F).

The series of collections cited below appears to represent a different hybrid population limited to the state of Sinaloa and found only in the coastal areas. The probable parents are *Coccoloba barbadensis* Jacq. and *C. uvifera* L., although in general the leaves are smaller than in either of these. Leaf texture, as well as the size and shape of the fruit, indicate a relationship to *C. barbadensis*. The leaf shape, especially at the base and apex of the blade, and the venation show similarities to *C. uvifera*. However, in contrast with most of the recognized *C. uvifera* hybrids from the West Indies and with *C.* × *lundellii* of Central America, *C. uvifera* seems to be the less dominant parent in this hybrid. Fruits of two types have been found, one essentially globose but strongly coronate and the other more or less oblong and obtusely to slightly coronate at the apex. The first type closely approaches the fruit of *C. barbadensis* and all fruits opened have fully developed embryos and endosperm. The second type shows the influence of *C. uvifera* and all fruits examined had either rudimentary seed development or were sterile.

Mexico. SINALOA: Altata, *Rose 1359* (NY); Culiacán, *J. Gonzalez Ortega 6583* (DS, GH, M), *Palmer 1518* (GH, NY); Elota, *J. Gonzalez Ortega 5879* (DS, GH, M); La Concha, *Gentry 6804* (F, GH); Mazatlán, *Howell 10559* (A), *Rose, Standley & Russell 14035* (NY); Villa Union, *Rose, Standley & Russell 13953* (NY); locality unspecified, *J. Gonzalez Ortega 7203* (F).

Most of these specimens were identified as *Coccoloba goldmanii* or *C. masoni*. The former is a distinct species, but is known from the type and one other collection. It may, in fact, be related here as part of this hybrid population or be one of the parents in place of *C. barbadensis*. *Coccoloba* needs a special study in Sinaloa and southern Chihuahua. *Coccoloba masoni* Lundell is clearly referable to typical *C. barbadensis* Jacq.

Coccoloba belizensis Standley, Trop. Woods **16**: 38. 1928.

Coccoloba hirsuta Standley, Publ. Field Mus. Bot. **4**: 303. 1929.

Coccoloba belizensis Standley is a clearly defined species and one which is easily recognized. The relatively large, globular terminal buds with tawny to chestnut-brown pubescence are distinctive even on sterile or adventitious shoots. The pubescent inflorescence is branched and consists of racemes arranged as a panicle of nearly equal branches. The leaf size varies considerably in fertile material as well as on sterile shoots which are presumably adventitious. Both staminate and pistillate plants are represented in the collections cited. The mature achene is surrounded by a fleshy perianth which seems to be formed by the equal enlargement of the perianth lobes and the hypanthium.

In the Berlin Herbarium there is a specimen studied by Gross which bears an unpublished herbarium name honoring the collector, Campbell. Much of Gross' work on *Coccoloba* appeared as small notes in miscellaneous

papers. Thus it is possible that this specific name has been published and, if so, it antedates *C. belizensis*.

Coccoloba hirsuta Standley was based on sterile material. The type, *Standley 54802*, as well as the cotype *52823*, was collected in the Lancetilla Valley, near Tela, Honduras. Standley noted the undesirability of basing species on sterile material, but felt that this species was easily recognizable by the "copious long pubescence of the leaves." In their treatment of the genus *Coccoloba* for the Flora of Guatemala (Fieldiana Bot. 24: 114. 1946) Standley and Steyermark continued to recognize *C. hirsuta* as a distinct species, referring to, but not citing additional specimens from, Guatemala and thus extending the range. I have seen two collections from the Department of Izabal, *Steyermark 38185* and *Standley 72945*, which are among those which must have been seen by Standley and Steyermark. These authors suggest that *C. hirsuta* "will be found to have panicled racemes, and to be closely related to *C. Tuerckheimii*." I am unable to distinguish between material annotated "*C. hirsuta*" by Standley and Steyermark and cited by Standley and that of occasional sterile specimens which the same authors assigned to *C. belizensis*. Such collections as *C. & W. von Hagen 1344* from the Department of Colón, Honduras, and *Lundell 2756* from the Department of Petén, Guatemala, approach *C. hirsuta* in the amount and type of pubescence. The Von Hagen collection is sterile and was taken from a 75–100-foot tree. This specimen may be an adventitious shoot comparable to the type of *C. hirsuta*, for the terminal bud is the same in size and shape, but there is less copious pubescence on the stem and much less on the leaves. The Lundell collection grades easily into fertile material which can be clearly defined as *C. belizensis* and which is found in the same area.

Guatemala. ALTA VERAPAZ: Chirreacté, *Standley 91620*, *91672* (F); between Sachaj and Sacacac, *Steyermark 45157a* (F). IZABAL: between Bananera and La Presa in Montaña del Mico, *Steyermark 38185*, *38186* (F); Escoba, *Standley 72945* (F). PETÉN: La Libertad, *Lundell 3463* (F, MICH); Monte Santa Teresa, *Lundell 2736* (F), *2756* (MICH). **British Honduras.** COROZAL DISTRICT: San Roque, *Gentle 554* (F); Corozal, Orange Walk Rd., *Gentle 4967* (F, MICH); Corozal, Pachacan Rd., *Lundell 4784* (A, F, MICH). EL CAYO DISTRICT: San Agustin, *Lundell 6812* (F, GH, MICH). ORANGE WALK DISTRICT: Honey Camp, *Lundell 637* (DS, F, GH, MICH, US). STANN CREEK DISTRICT: Carib Reserve, *Gentle 3088* (MICH); Mullins River, *Gentle 3365*, *3369* (A, MICH); Silk Grass Creek Reserve, *Gentle 2982* (MICH); Stann Creek, *Gentle 2964* (A, MICH); Stann Creek Valley, *Stevenson 7* (US-holotype; A, F, Y). TOLEDO DISTRICT: Jenkins Creek, *Gentle 4080* (A, MICH). District unspecified: Belize, *Campbell 117* (B); Crique Negra, *Stevenson 104* (F, Y); All Pines, *Schipp 794* (A, F, GH, MICH); Tower Hill Estate, *Karling 14* (F, GH). **Honduras.** ATLÁNTIDA: Lancetilla Valley near Tela, *Howard, Briggs, et al. 451* (A), *Standley 52823* (F), *53555* (A, F), *54802* (F-type of *C. hirsuta*; A); San Alejo, *Standley 7971* (F); San Juan near Tela, *Yuncker 4817* (A, F, MICH); Tela, *Standley 53402* (A, F). COLÓN: Guarunta, *C. & W. von Hagen 1344* (F). **Nicaragua.** Eastern Nicaragua, *Shank 93* (Y).

Coccoloba caracasana Meisner, DC. Prod. **14**: 157. 1856.

Coccoloba caracasana forma *glabra* Lindau, Bot. Jahrb. **13**: 211. 1890.

This species was formerly considered to have orbicular leaves, but the large number of specimens examined indicates that a broadly oblong leaf is more characteristic than a strictly orbicular one. Considerable variation in leaf size and shape is found in the species. Leaves of adventitious shoots may have nearly ovate blades up to 34 cm. long and 28 cm. wide on petioles to 4 cm. long. The straw-colored ocreolae are membranaceous, with several occurring at each nodule because of the presence of numerous flowers, several of which are frequently aborted. In fruit the lobes of the perianth expand to cover more than the upper half of the achene.

The forma *glabra* which Lindau described is scarcely worthy of recognition since the density and persistence of the pubescence varies in single collections and on single plants.

In addition to the specimens cited below, the species is known from Venezuela and Colombia and possibly farther south along the Andes. The type has been cited both as *Humboldt 732* and as *Bonpland 732*. One collection cites only Caracas, Venezuela, as the locality, while another bears a label referring to the "valley of Araguensibus."

México. CHIAPAS: Las Garzas, Acapetagua, *Matuda 2677* (A, DS, F, MICH), *2806* (A, MICH); Mapastepec, *Matuda 17516* (F); Tapachula, *Matuda 17704* (F). **Guatemala.** ESCUINTLA: Iztapa, *J. R. Johnston 1171* (F); San José, *Standley 64232* (F, MICH), *64019*, *64190* (F). JUTIAPA: Between Trapiche Vargas & Asunción Mita, *Steyermark 31792* (F). RETALHULEU: Between Nueva Linda and Champerico, *Standley 87673* (F). SANTA ROSA: Santa Rosa, *Ørsted 668* (M); Capulín, *Standley 79592* (F); Los Cerritos region, Capulín, *Standley 79607*, *79563* (F, MICH). SUCHITEPÉQUEZ: Tiquisate, *Steyermark 47700* (F). **El Salvador.** LA PAZ: Zacatecoluca, *Calderon 305* (GH). LA UNIÓN: Laguna de Maquigüe, *Standley 20977* (GH). SAN MIGUEL: San Miguel, *Standley 21139* (GH); Laguna Jaguay, San Miguel, *Fassett 28813* (A); Laguna de Olomega, *Standley 20990* (GH). SAN SALVADOR: San Salvador, *Renson 139* (NY), *Standley 23611* (F, GH). SAN VICENTE: San Vicente, *Standley 21261* (F, GH), *Standley & Padilla 3702* (F). SANTA ANA: Hacienda la Barra, *Carlson 1031* (F). SONSONATE: San Antonio del Monte, *Standley 22171* (GH). **Nicaragua.** CHINANDEGA: Chichigalpa, *Standley 11187*, *11334* (F). CHONTALES: Juigalpa, *Standley 9302*, *9305* (F). GRANADA: Granada, *Baker 2435* (A, MICH). LEÓN: La Paz, *Baker 2272* (GH). Locality unspecified: *C. Wright s.n.* (GH); *Ørsted 670*, *671* (C). **Costa Rica.** GUANACASTE: between Bebedero and Taboga, *Brenes 12562* (F); Filadelfia, *Echeverria 295* (F); Nicoya, *Tonduz 13799* (F, G, GH), *13974* (G, GH); Isla de Chira, *Valerio 1467* (F); Santa Ana de Nicoya, *León 989* (F). Province unspecified: Los Loros, *Brenes 22056* (F). Locality unspecified: *Hoffmann 292* (B), *Warscewicz s.n.* (B). **Panamá.** CANAL ZONE: Ancón, *Pittier 2730* (US); Gorgas Memorial Laboratory grounds, *White 106* (F, GH, MO); Río Agua Salud near Frijoles, *Piper 5848* (GH); Victoria Fill near Miraflores Locks, *Allen 1701* (F, GH, MO, NY). CHIRIQUÍ: Progreso, *Cooper & Slater 270* (F). LOS SANTOS: La Jagua, *Bartlett & Lasser 16382* (MICH). PANAMÁ: Sabanas Road, *Gillespie P-34*, *P-34a* (DS); Chepo, *Kluge 25* (F, NY).

Coccoloba chiapensis Standley, Proc. Biol. Soc. Wash. 33: 67. 1920.

Coccoloba anisophylla Standley, Publ. Field Mus. Bot. 4: 303. 1929.

Coccoloba anisophylla was based on sterile material, but Standley reported that "the form of the leaves is quite different from that of any other Central American species." On studying the material cited by Standley and being unable to distinguish *C. chiapensis* from *C. anisophylla*, I have referred the latter to the synonymy of *C. chiapensis*. This species is distinct in having leaves which are oblong to elliptic, broadest near the middle, tapering to an acuminate apex and narrowing to an abruptly obtuse and asymmetrical base. Only staminate flowers are known for this species and additional material is needed. Sterile specimens may resemble *C. novogranatensis* but can be distinguished by the basal origin of the petiole and by the pubescence.

México. CHIAPAS: Finca Irlanda, *Purpus 7699* (US-holotype of *C. chiapensis*; B, GH, NY); location unspecified, *Purpus 7599* (GH, NY). **Honduras.** ATLÁNTIDA: Lancetilla Valley near Tela, *Standley 53260* (F-holotype of *C. anisophylla*; A), *53364*, *54840* (A, F).

Coccoloba cozumelensis Hemsley, Biol. Am. Centr. 4: 108. 1887.

Coccoloba yucatana Lindau, Bot. Jahrb. 13: 190. 1890.

Coccoloba cozumelensis is readily recognized but difficult to define and separate in a key. The species seems amply distinct on the basis of the pale tan color of the leaves which often dry a lighter yellow-brown on the lower surface, and the sessile fruits which are obtuse at the apex with the perianth lobes not at all coronate. Also, the petioles are puberulent and along the midrib and veins on the lower leaf surface there is a characteristic crispate pubescence.

Some specimens of *Coccoloba cozumelensis* grade into the Central American phase of *C. swartzii* and it is possible that a hybrid complex exists in coastal areas where these species occur together. Since I have insufficient material to resolve this problem, the key characteristics used here apply to plants represented by the distinctive holotypes of each.

Two recent collections from the state of Chiapas are referred here. One collection, *Margery C. Carlson 2071*, made at Tuxtla Gutiérrez, is annotated as a new species by Standley and Williams. The name used refers to the tenuous spike. This collection, in flowering condition, is intermediate between typical material of *C. cozumelensis* and specimens referred to *C. spicata*, but other than the larger leaves of *Carlson 2071*. I find no reason for recognizing the collection as a new species. The second collection, *Dressler 1408*, from El Real, Chiapas, is intermediate between typical *C. cozumelensis* and the Carlson collection.

Standley placed *Coccoloba yucatana* in the synonymy of *C. cozumelensis*. I have re-examined authentic material of this and confirm his decision.

México. CAMPECHE: Tuxpeña, *Lundell 853* (A, DS, F, GH, MICH). CHIAPAS:

Tuxtla Gutiérrez, *Carlson 2071* (F, NY); El Real, east of Ocosingo, *Dressler 1408* (GH). QUINTANA ROO: Cozumel, *Gaumer 18* (B-holotype of *C. yucatana*; GH, K); Cobá, *C.L. & A.A. Lundell 7804* (A, DS, F, M, MICH), *7830* (A, DS, F, MICH). TABASCO: Reforma, Balancán, *Matuda 3173* (A, MICH). **British Honduras.** BELIZE DISTRICT: Maskall, *Gentle 1068* (A, F, GH, MICH), *1349* (A, F, MICH). COROZAL DISTRICT: San Antonio, *Bartlett 13031* (A, F, MICH), *Lundell 4815* (A, F, MICH); Corozal, *Gentle 524* (F, MICH). EL CAYO DISTRICT: Little Mountain Pine Ridge, *Bartlett 13060a* (MICH); Mountain Pine Ridge, San Agustín, *Lundell 6648* (DS, F, GH, MICH). ORANGE WALK DISTRICT: Honey Camp, *Meyer 50* (*F*). **Guatemala.** IZABAL: Río Dulce, *Wilson 387* (F). PETÉN: Carmelita. *Egler 42–249* (F); La Libertad, *Lundell 3570* (F, GH, MICH).

Coccoloba darienensis, sp. nov.

Arbor, 12 m., ramulis teretibus, glabris; ocreis chartaceis, oblique truncatis, 1 cm. longis, glandulis (?) resinosis, adpressis; petiolis ad basem ocreis gerentibus, teretibus, supra canaliculatis, glabris, 7–11 mm. longis; laminis anguste oblongis vel lanceolati-oblongis, apice acutis vel breviter acuminatis, basi acutis, 10.5 × 3.5 vel 14.5 × 5 cm. longislatisque glabris, tenuiter coriaceis, nerviis primariis 9 vel 10, arcuato-adscendentibus; inflorescentibus racemosis, 8–14 cm. longis, floribus crebris, nodulis confluentibus, pedunculis 1 cm. longis, rachis striatis, puberulentibus; floribus ignotis, bracteis ovatis vel oblongis, apice obtusis, 1 mm. longis, puberulentibus vel breviter pilosis, ocreolis membranaceis, raro bracteolisque puberulentibus vel apice ciliatis; pedicellis fructiferis 1 mm. longis, glabris; fructu ovoideo basi rotundato, 5–6 mm. longo, 5 mm. diametro, obtuse trigono, hypanthio non manifesto, lobis perianthii ad basem distinctibus, late ovatis, imbricatis, acheniis nitidis, nigris.

Panamá. DARIEN: Pinogana, *P. H. Allen 934* (GH-type; F, MO).

This collection had been identified as *Coccoloba acuminata*, which is certainly a related species. The strongly divided fruiting perianth would allow this species to be placed in Lindau's section *Campderia*. *Coccoloba darienensis* is distinct from *C. acuminata* on the many-flowered inflorescence in which the flowers are confluent, not clustered, and the axis is terete but striate or grooved and not swollen below each nodule. Furthermore, *C. darienensis* differs in the evident fruiting pedicels, while *C. acuminata* can be regarded as having only spicate inflorescences without evident pedicels in fruit.

Coccoloba diversifolia Jacquin, Enum. Pl. 19. 1760.

Coccoloba laurifolia Lundell, Bull. Torrey Club 66: 594. 1939, and authors, possibly Jacquin, Hort. Schoenbr. 3: 9, *t. 267*. 1798.
Coccoloba lancifolia Lundell, Bull. Torrey Club 66: 593. 1939.

I have previously discussed the proper application of the epithet *Coccoloba diversifolia* Jacq. (Jour. Arnold Arb. 30: 421–424. 1949). All recent publications, however, have used *C. laurifolia* Jacq. for material more prop-

erly called *C. diversifolia*. *Coccoloba laurifolia*, based on material from Caracas, Venezuela, was described and illustrated by Jacquin, but I have been unable to find any collections from northern South America which exactly duplicate the characteristics which he illustrated. It is probable that *C. laurifolia* is the same as *C. diversifolia*, described by Jacquin twenty-eight years earlier. Oddly enough, no specimens of this which could be attributed to Jacquin have been seen in European herbaria, although a few specimens collected from cultivated plants and labelled "*C. laurifolia* Jacq." are present in the herbaria at Berlin, Leningrad and Geneva. However, all of these are true *C. diversifolia* and fail to compare favorably with the original illustration of *C. laurifolia* Jacq.

Lundell compares *Coccoloba lancifolia* with the original description of *C. laurifolia*, reporting that his new species differs in its small, lanceolate and pointed leaves. *Coccoloba diversifolia*, as its name implies, is a variable species in respect to leaf shape, but in all the characteristics which I can observe, it is the same as *C. lancifolia*. In their treatment of the genus for Guatemala (Fieldiana Bot. 24: 114. 1946), Standley and Steyermark placed *C. lancifolia* Lundell in synonymy of *C. laurifolia*, but without comment. I concur with their decision, but call the species *C. diversifolia* Jacq. The small leaf size and the pointed apex can be found in many populations of *C. diversifolia*, especially in Cuba, the Bahamas and the Florida Keys.

This is the first time that this common West Indian species has been recognized in Central America and Mexico.

México. QUINTANA ROO: Lago San José, *Frère Arsène s.n.* (B). SAN LUIS POTOSÍ: Tamazunchale, *Edwards 921* (F). **Guatemala.** ALTA VERAPAZ: Cerro Cinajá, *Steyermark 45669* (A, F, MICH). IZABAL: Bay of Santo Tomás, *Steyermark 39232* (F), *39351* (F, MICH), *39357*, *39363* (F).

British Honduras. COROZAL DISTRICT: Location unspecified, *Gentle 231* (F, MICH, NY); Consejo, *Lundell 4945* (F, MICH). District unspecified: Jacinto Hills, *Schipp 1200* (MICH-holotype of *C. lancifolia*; A, GH, W).

Coccoloba emarginata Jacquin, Enum. Syst. Pl. 37. 1760.

This species was described by Jacquin in 1760 and illustrated in his Observationum Botanicarum in 1764 (*tab. 9*). It is based on a specimen from the herbarium of Mygind but no locality is given. The species was compared with the Hispaniolan *Coccoloba leoganensis* Jacq., which I have recognized (Jour. Arnold Arb. 39: 28–30. 1958), but which is better known in that flora as *C. rotundifolia* Meisn., a later homonym. Lindau was unable to place the Jacquin species and so listed it as of uncertain identity.

The situation here is similar to that of *Coccoloba barbadensis*. The specimen which Jacquin described must have come from the Yucatán Peninsula of Mexico. The illustration, although of a sterile plant, is an excellent one and is obviously the same as *Neomillspaughia emarginata* (Gross) Blake (Bull. Torrey Club 48: 84. 1921), the basionym of which is *Podopterus emarginatus* Gross (Repert. Sp. Nov. 12: 218. 1913). Gross' species is

based on *Seler 5600* from Yucatán, Mexico. Since the combination has already been made, I can only add *Coccoloba emarginata* Jacquin to the synonymy of *Neomillspaughia emarginata* (Gross) Blake and thereby dispose of a troublesome and misplaced ancient epithet in the genus *Coccoloba*.

Coccoloba goldmanii Standley, Contr. U.S. Nat. Herb. 23: 245. 1922.

This distinctive species from the drier areas of northern Mexico has not been recollected in the past sixty years. Cited below are the Goldman collection made in 1898 and the Hartman collection made in 1891. The latter was misidentified as *Coccoloba orizabae*. *Coccoloba goldmanii* is recognized by the nearly orbicular leaves which are persistent short pubescent below and which possess a conspicuous network of veins on the lower surface. The flowers are unknown. The ellipsoidal fruits are not coronate and the lobes of the fruiting perianth cover the upper half of the achene, the hypanthium the lower half.

México. CHIHUAHUA: Apajcachi, *Hartman 535* (GH). SINALOA: Valley of Río Fuerte, *Goldman 245* (US-holotype; GH).

Coccoloba hondurensis Lundell, Bull. Torrey Club 66: 591. 1939.

Coccoloba marginata J. Donnell Smith, Enum. Plant. Guat. 6: 36. 1903, not Benth.

In describing this species, Lundell states, "the specimens show considerable variation, especially in leaf shape, inflorescence, and fruits but all appear to be referable to a single species. . . . Collections of *C. hondurensis* have been referred to *C. Schiedeana* Lindau, *C. marginata* Benth., *C. barbadensis* Jacq., and *C. leptostachya* Benth. I have not been able to associate the species with any of these."

It is unfortunate that Lundell did not state how he distinguished *C. hondurensis* from the other species he lists. Standley and Steyermark (Fieldiana Bot. 24: 116. 1946) refer *C. hondurensis* to the synonymy of *C. schiedeana* Lindau in their treatment of the genus for Guatemala. I regard *C. schiedeana* Lindau as identical to *C. barbadensis* Jacq. I hesitate to follow Standley and Steyermark in reducing *C. hondurensis*, for there is a problem here which I cannot solve, even with abundant herbarium material. I prefer to keep *C. hondurensis* as a distinct species and to call this problem to the attention of field workers for further study. Material cited below as *C. hondurensis* is easily recognized, but difficult to define or to separate in a key. For the present, *C. hondurensis* can be recognized when dry by the dark brown or black upper leaf surface which contrasts with the lighter-colored lower surface. The inflorescences are usually twice as long as the subtending leaves. The fruiting pedicels are slightly more tenuous and seem relatively longer than those of *C. barbadensis* and the apex of the fruit, while coronate, is more obtuse than is general in *C. barbadensis*. Usually such distinctions are not valid in this difficult genus and I am maintaining this as a distinct species for temporary convenience only.

Further study should be rewarding, for *C. hondurensis* may prove to be either a variety of *C. barbadensis* or of hybrid origin.

México. OAXACA: Tehuantepec, *L. Williams 9906* (Y). VERACRUZ: Fortuno, Coatzacoalcos River, *L. Williams 8701* (Y). **Guatemala.** ALTA VERAPAZ: Río Sebol, near Carrizal, *Steyermark 45785* (F). IZABAL: Quiriguá, *Standley 23867, 23988, 24547, 24601* (GH), *72249* (F); Puerto Barrios, *Standley 72143* (F); Salomón Creek, south of Bananera, *Steyermark 38934* (F). PETÉN: Río Cancuén, *Steyermark 45925* (A, F); Río Machaquilla, north of El Cambio, *Steyermark 45928* (F).

Honduras. ATLÁNTIDA: Vicinity of Tela, *Bangham 212* (A); *Chickering 233* (F, MICH), *Howard, Briggs et al. 452, 503, 504, 505, 506, 507* (A), *Salvoza 810* (A), *Standley 53716, 54476, 54481, 54752, 56598, 56659* (A, F); La Ceiba, *Yuncker, Koepper & Wagner 8295* (F, GH). COLÓN: Cuyamel, *Carleton 598* (US). SANTA BÁRBARA: San Pedro Sula, *J. Donnell Smith 5433* (A, F, GH, M). Dept. unspecified: Puerto Sierra, *Wilson 74* (NY), *562* (F, GH, NY).

British Honduras. BELIZE DISTRICT: Quamina Creek, Manatee, *Gentle 3437* (A, MICH); Cornhouse Creek, Manatee River, *Bartlett 11275* (F, MICH); Sibun River, *Bartlett 11361* (GH, MICH); Northern River, *Gentle 897* (A, F, MICH). EL CAYO DISTRICT: Little Cocquericot, Belize River, *Lundell 3995* (MICH), *3996* (MICH-holotype; F), *3997* (GH, MICH). STANN CREEK DISTRICT: Sarawee Pine Ridge, *Gentle 2699* (A; F, MICH), *2748* (A, F, MICH); Mullins River Road, *Gentle 2731A* (A, F, MICH); Carib Reserve, *Gentle 2734* (A, F, MICH), *s.n.* (A, MICH, WIS); Stann Creek Valley, *Gentle 2733* (A, F, MICH), *2735* (A, F, MICH, WIS), *2737, 2738* (A, F, MICH), *s.n.* (MICH); Middlesex, *Gentle 2820, 2874, 2878, 2887* (A, MICH), *3011, 3018* (A, F, MICH); Silk Grass Creek Reserve, *Gentle 2989* (A, MICH); Big Eddy Ridge, *Gentle 3348* (A, MICH); Mt. Cow Vayyel, *Gentle 3538* (A, MICH); Silk Grass Creek Reserve, *Record BH-20* (Y); Middlesex, *Schipp 453* (A, F, GH, MICH). TOLEDO DISTRICT: Swasey Branch, Monkey River, *Gentle 3716, 3584* (A, MICH). District unspecified: Manatee Lagoon, *Peck 255* (GH).

Coccoloba humboldtii Meisner, DC. Prodr. **14**: 163. 1856.

Coccoloba orizabae Lindau, Bot. Jahrb. **13**: 189. 1890.

Coccoloba humboldtii var. *longipedicellata* Gross, Repert. Sp. Nov. **12**: 219. 1913.

Coccoloba petrophila Brandegee, Univ. Calif. Publ. Bot. **10**: 404. 1924.

Meisner cited two collections in the original description of this species, *Humboldt 4484*, which is in the Willdenow Herbarium as No. 7705, and *Berlandier 105*, collected near Tampico. Although the Humboldt specimen in the Willdenow herbarium at Berlin bears no specific locality beyond "Mexico," this should be selected as the lectotype. A second specimen collected by Humboldt is in the Paris herbarium and bears the number *4484*, with the locality given as "Vera Cruz." Unhappily, this specimen was identified and annotated by Lindau as *Coccoloba nutans*, an entirely different species.

Coccoloba orizabae Lindau was distinguished by Lindau in a key to the species on the shape of the leaf blade, especially the narrowed base and the

acuminate apex. The type of this species was *Bourgeau 2822* from Orizaba, Veracruz.

Gross distinguished his new variety *Coccoloba humboldtii* var. *longipedicellata* by the longer pedicels and the inflorescence rachis as long as the leaves. Gross failed to appreciate the dioecious character of the species and based his variety on a staminate plant, in contrast to the holotype, which is a pistillate plant. The variety is clearly included within the range of variation of the Humboldt type collection and, as more recent collections demonstrate, should be included within the species.

Coccoloba petrophila was described by Brandegee in a report on Purpus collections from Mexico. *Purpus 8872* from Camerón, Veracruz, was selected as the type. No discussion was given of the distinctions or affinities of the species. Another collection, *Purpus 8736*, made at the same time and location, was not seen, or at least not cited, by Brandegee. Subsequently Purpus collected additional material assigned to this species from near Los Conejos (*16425*, *16430*) and Rancho Remudadero (*10967*). The last number was suggested to be a wide-leaved variety in Brandegee's herbarium notes. These Purpus collections, together with *Seler 4482*, show the extremes of variation to be expected in *C. humboldtii*, as well as the intermediate forms which made a continuous series from former concepts of *C. humboldtii* to *C. petrophila* and *C. orizabae*. Several of the Purpus collections also show thin-textured immature leaves of varying sizes and shapes. It is in such specimens as *Purpus 16425* that transitions to the thin-textured acuminate-tipped leaves of *C. orizabae* can be found.

In his treatment of the trees and shrubs of Mexico, Standley places both *Coccoloba orizabae* and *C. humboldtii* in a division of his key headed "rachis of the inflorescence glabrous." In all of the material cited below, the young inflorescence rachis is subtomentose, but at maturity is puberulent or glabrate. The same is true of the ocreae. The original descriptions of the three species and the variety fail to mention pubescence.

México. San Luis Potosí: Las Canoas, *Pringle 5111* (A, GH). Veracruz: Tampico, *Berlandier 105* (A, B, LE, P), 201 (LE), *Palmer 322* (GH, NY); Veracruz, *Galeotti 109* (BR), *Juzepczuk 1116* (F, LE), *Gorrin s.n.* (LE); Colipa, *Karwinsky s.n.* (LE); Laguna Tamiahua, *LeSueur 100* (GH), *101* (F); Orizaba, *Bourgeau 2822* (B-holotype of *C. orizabae*; P); Pánuco River near Ebano, *LeSueur 102* (F, GH); Pacho, *Liebmann s.n.* (LE); Coatzacoalcos, *Orcutt 3162* (DS, F, GH); Pueblo Viejo, *Palmer 443* (F, G, GH, NY); Camerón, *Purpus 8736* (GH, NY, US), *8872* (GH-isotype of *C. petrophila*); Rancho Remudadero, *Purpus 10967* (B, F); Zacualpan, *Purpus 12022*, in part (DS); Los Conejos, *Purpus 16425* (A, F, LE), *16430* (A, F); Puerto de Alvarado, *Seler 4482* (B-holotype of *C. humboldtii* var. *longipedicellata*; GH); Mocambo, *Troll 59* (M); Alvarado, *Schubert & Rojas 1844a* (A); location unspecified, *Humboldt 4484* (B-Herb. Willd. 7705, lecto*type*; P).

Coccoloba lasseri Lundell, Contr. Univ. Mich. Herb. 6: 10. 1941.

This species is regarded as endemic to Panama and is perhaps not distinct from *Coccoloba tuerckheimii* Donn. Sm. For the present, *C. lasseri*

may be recognized by the paniculate inflorescence of few branches, the leaves with short, stout petioles and the blades which, while narrowed below the middle, are truncate or abruptly rounded at the base. Finally, the fruits known for *C. lasseri* are rounded at the base. In contrast, *C. tuerckheimii* has a paniculate inflorescence of many more branches, leaves with longer, tenuous petioles and blades cuneate at the base with fruits narrowed to a short stipe at the base.

Panamá. COCLÉ: Aguadulce, *Pittier 4989* (F); Penonomé, *Williams 357* (NY). HERRERA: Chitré, *Allen 1111* (F, GH, MO); Mangle Bejuco, *Steyermark, Allen & Dodge, s.n.* (F). PANAMÁ: Bejuco, *Allen 2542* (A, F); Panamá Nat. Highway, Las Lajas Bridge, *Bartlett & Lasser 16638* (MICH); Río Pacora, *Bartlett & Lasser 16946* (MICH-holotype); Balboa to Chamé, *Dodge, Hunter, Steyermark & Allen 16732* (MO); Punta Paitilla, *Standley 26265* (A). Province unspecified: *Duchassaing s.n.* (P).

Coccoloba liebmannii Lindau, Bot. Jahrb. 13: 189. 1890.

Coccoloba lapathifolia Standley, Contr. U.S. Nat. Herb. 23: 245. 1922.

This species is quickly and easily recognized by the persistent pubescence on the lower leaf surface. Most of the leaves show a tendency toward an undulate or wavy margin to the blade, while in some specimens this tendency is so exaggerated that the marginal folds overlap in the dried specimens. The fruit is globose and the perianth lobes are imbricate in fruit. The achene is not coronate.

Standley distinguished his new species, *Coccoloba lapathifolia*, from *C. liebmannii* on the basis of a "glabrous or very minutely puberulent" inflorescence rachis, in contrast to one densely short-pilose. Examination of the material cited below, however, including both types, indicates quite clearly that *C. lapathifolia* is the same as *C. liebmannii* and should be placed in synonymy.

México. COLIMA: Manzanillo, *Ferris 6061* (A, DS, F), *Palmer 965* (GH, NY); between Galera and Pochutla, *Liebmann s.n.* (C-holotype of *C. liebmannii*; B). GUERRERO: Acapulco, *Palmer 206* (US-holotype of *C. lapathifolia*; GH); Placeres, *Hinton 9101* (NY). OAXACA: Distrito de Tamiltepec, *Conzatti 4406½* (GH); Llano Grande & Pinotepa, *Nelson 2341* (GH); Cerro de Picacho, *Purpus 7735* (GH, NY); Tequisistlán, *Seler 1719* (B).

Coccoloba lehmannii Lindau, Bot. Jahrb. 20 (Beibl. 49): 7. 1895.

Uvifera lehmanni Lindau, in footnote, l.c.
Coccoloba lehmanni Lindau, Repert. Sp. Nov. 1: 156. 1905.
Coccoloba changuinolana Standley, Publ. Field Mus. Bot. 8: 9. 1930.
Coccoloba williamsii Standley, Publ. Field Mus. Bot. 11: 148–149. 1936.
Coccoloba allenii Lundell, Contr. Univ. Mich. Herb. 6: 8. 1941.

Lindau described this species in two papers. In the earlier publication the specific name is spelled "*lehmannii*" and in the later one, "*lehmanni*." Two collections (*Lehmann 6109* and *7560*) were cited in the first publication, but in the second description only *Lehmann 7560* was cited. In both

descriptions this new species is compared with *Coccoloba gracilis* of the section *Campderia*. Lindau's two descriptions of *Lehmann 7560* are comparable; thus one may assume that Lindau overlooked the first publication which described both of these collections. It seems desirable to select *Lehmann 7560* in the Berlin Botanic Garden Herbarium as the lectotype.

Coccoloba changuinolana was based on three collections from Panama with *Dunlap 499* being selected as the type. An examination of these specimens shows Standley's original description to be in error on the important character of "perianthii tubo accrescente inclusus." The perianth lobes, not the perianth tube, increase in size to surround the mature achene, and the species as represented by the collections cited by Standley belongs to the section *Campderia*. Although Standley stated that the new species was related to *C. schiedeana*, I can find no basis for comparison between the two. However, *C. changuinolana* is comparable in all characteristics with *C. lehmannii*, from Columbia, and is assigned in synonymy to that species.

I have seen only the type collection, *Llewellyn Williams 4803*, of the several specimens that Standley cited in his original description of *C. williamsii*. This Peruvian species must also be placed in the synonymy of *C. lehmannii*. *Williams 4803* is in fruiting condition and the longer fruiting pedicels are in contrast to the shorter pedicels found on the flowering specimens of the Lehmann collection which is the type of the species. Additional collections which I have seen are intermediate. Standley indicated a relationship of *C. williamsii* with *C. caracasana*, both species being assigned to the section Campderia, but these are clearly distinct in the leaf shape and nature as well as in the abundant pubescence.

Still a third species, *Coccoloba allenii* Lundell is assigned to synonymy here. Lundell correctly noted the alliance of *C. allenii* with *C. williamsii*, but distinguished *C. allenii* on the basis of a furfuraceous-lepidote indument and large apiculate spathaceous ochreolae. Additional specimens collected by Allen in Panama show many intermediate conditions in both characteristics.

Coccoloba lehmannii is currently known to occur in Columbia (type), Panamá, Peru, Costa Rica and Venezuela.

Costa Rica. La Palma, Suxaola Valley, *Dunlap 467* (F, Y). **Panamá.** BOCAS DEL TORO: Daytonia farm, Region of Almirante, *Proctor Cooper 421* (F, Y); Changuinola Valley, *Dunlap 499* (F-type of *C. changuinolana;* B, Y). COCLÉ: El Valle, *Allen 2181* (MICH-type of *C. alleni*; A, F), *Allen & Alston 1857* (F, GH, MO).

Coccoloba lindaviana, sp. nov.

Frutex, 8 m., ramulis teretibus, leviter striatis, glabris; ocreis coriaceis, dense strigosis vel glabratis, 9–12 mm. longis; petiolis supra basem ocrearum gerentibus, 8–11 mm. longis, glabris; laminis oblongis, anguste oblongis vel oblongi-ellipticis, apice acutis vel breviter acuminatis, basi rotundatis, vel truncatis, 15 × 4.5 vel 22 × 8.5 cm. longislatisque, cori-

aceis, glabris, nerviis primariis 11–15, adscendentibus; inflorescentiis terminalibus, racemosis 12–15 cm. longis, rachis glabris, bracteis triangularibus, minutis, minusque 0.5 mm. longis, glabris, ocreolis membranaceis, glabris vel ciliatis ad marginem, bracteis aequaliter; floribus ignotis; pedicellis fructiferis 1.5–2 mm. longis, glabris; fructu ovato, 8 mm. longo, 6 mm. diametro, ad apicem obtuse coronato; acheniis castaneis, levibus, nitidis.

Honduras. YORO: Aguan river valley, vicinity of Coyoles, *Yuncker, Koepper & Wagner 8032* (GH-holotype; F); Cortés, canyon of Rio Piedras, 3 km. from San Pedro Sula, *Molina 3430* (F); El Encanto in Montana La Cumbre, *Molina 3577* (F); Montana de Rio Piedras, *Molina 3555* (F).

The Molina collections bear an unpublished name attributed to Standley and L. Williams. I agree with them that a new taxon is represented here, even though this species is currently known only from old and fruiting specimens. *Coccoloba lindaviana* is, therefore, distinct on the basis of the leaf shape, the position of the leaves, which are borne above the base of the ocreae, and by the oval fruit which is slightly coronate at the apex. It is also similar to *C. hondurensis*, differing in the venation of the leaves and the position of the petiole base. All of the fruits I have examined had fully-formed seeds. Nevertheless, there is a possibility of a hybrid origin of this species.

The species is named in honor of Gustav Lindau who published a monograph of the genus *Coccoloba* in 1890.

Coccoloba lindeniana (Bentham) Lindau, Bot. Jahrb. 13: 82. 1890.

Campderia lindeniana Bentham, in Benth. & Hook. Gen. Pl. 3: 103. 1880.

This species is known only from the type collection made by J. Linden (*1602*) in Tabasco, near Teapa, Mexico, in May, 1840. An altitude of 300 m. is given on the collector's label. Specimens have been seen in the herbaria at Geneva, Leningrad and Paris, as well as a fragment in the Berlin herbarium.

Coccoloba lindeniana seems distinctive among Mexican and Central American species in the very pubescent leaves and inflorescence axis and the pubescence of the bracts and ocreolae. It may prove to be nothing more than the pubescent form of *C. acuminata* which Lindau described as *C. acuminata* var. *pubescens*. *Coccoloba acuminata* is widely distributed through Central America and adequately represented in herbaria, although only a few collections are available from Guatemala. The pubescent phase, which I do not recognize as a distinct taxon, is found throughout the range of the species. The abundance and persistence of the pubescence varies.

The inflorescence of *Coccoloba acuminata* is characteristically interrupted, with the axis swollen below each flower cluster. The clusters therefore appear at an acute angle to the inflorescence axis. In *C. lindeniana*

the axis is not swollen and the flower clusters appear to be produced flat on the axis.

The final position of *Coccoloba lindeniana* will await the collection of more material from Mexico. It is to be hoped that some of this will be in fruiting condition.

Coccoloba × lundellii Standley (pro sp.)

Coccoloba lundellii Standley, Publ. Field Mus. Bot. 8: 138. 1930.
Coccoloba suborbicularis Lundell, Lloydia 2: 84. 1939.

In the original description of *Coccoloba lundellii* Standley stated, "Evidently a relative of the widespread *C. schiedeana* Lindau, but differing conspicuously in its very broad leaves, somewhat suggestive of those of the common sea grape, *C. uvifera*."

A few years later Lundell described *Coccoloba suborbicularis* and reported that "among the species of the Yucatan Peninsula, *C. suborbicularis* is unique in having the leaf conspicuously unequal at the base."

The type of *Coccoloba lundellii* bears a few fruits, two of which were opened and found to be sterile. The type specimen of *C. suborbicularis* bears a few staminate flowers. Both holotypes show many of the characteristics of *C. uvifera*. The few fruits, the clustered flowers, the puberulence and the asymmetrical leaf base are characteristics of *C. uvifera*. The broad, orbicular leaves are dominant on all specimens seen, but a few smaller oblong leaves, with a strong development of secondary veins when dry, are suggestive of some other influence.

Several hybrids of *Coccoloba uvifera* and neighboring species have been found or suggested in the flora of the West Indies and it appears that a parallel situation is present here. It is not clear from the material on hand whether the second parent is *C. hondurensis,* which may, in turn, be a variation of *C. barbadensis,* or *C. reflexiflora*. Both species are known from the area of the hybrid.

British Honduras. ORANGE WALK DISTRICT: Honey Camp, coastal region, *Lundell 649* (F-holotype; DS, GH). STANN CREEK DISTRICT: Stann Creek Railway, *Gentle 2687* (MICH-holotype of *C. suborbicularis*; A, F); Stann Creek Valley, *Gentle 2716* (A, MICH); Middlesex, *Gentle 2877* (A, MICH), *2890* (A, MICH).

(To be concluded)